An historical review of the higher classification of the Noctuidae (Lepidoptera)

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Synopsis

An historical review of the development of the higher classification of the Noctuidae is presented, emphasising the interrelationships between the various systems that have been put forward and the taxonomic impact of the character complexes that have been employed. A provisional cladistic analysis of the higher noctuid taxa is performed and a tentative cladogram proposed. Many of the currently accepted subfamilies are rejected as potentially paraphyletic or polyphyletic assemblages. New, cladistic, definitions of the families Arctiidae and Noctuidae are suggested, which would necessitate the establishment of the Aganaidae and Herminiidae as separate families.

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Introduction

> It is exceptional to find any two authors who use the same combination of subfamily names within the Noctuidae (Nye, 1975: 10).

> The classification of this family [Noctuidae] rests in a state of great confusion, and few authors appear to hold similar views regarding the suprageneric taxonomy. I have concluded after spending much time (perhaps I should say wasting time) on the problem, that it is impossible to present . . . a correct suprageneric classification (Zimmerman, 1958: 197–198).

> The subfamily divisions . . . are on the whole natural, but their defining characters have far too many exceptions, and some genera may perhaps be completely misplaced (Forbes, 1954: 5).

> Much of the present grouping of species and genera is still debatable, and reasons for groupings are often obscure (Birch, 1972*a*: 189).

The moths of the family Noctuidae, sometimes known as 'owlets', constitute one of the three largest families of Lepidoptera. Estimates of the number of known species vary considerably but the most frequently quoted figure of 25,000 is still far in excess of such other groups as the butterflies (15,000–20,000) and the land-living vertebrates (about 18,000).

Not only are the noctuids a large family numerically, but they are also extremely important economically. The larvae of many genera (e.g. *Spodoptera, Heliothis, Euxoa, Earias* and *Trichoplusia*) are well known as army-worms, cutworms, bollworms and stem-borers and cause many millions of pounds' worth of crop loss each year. Their control, being at present primarily chemical, is also expensive. A predictive classification can thus be seen to be an essential prerequisite to the efficient use of the resources available to combat the pest species.

However, constructing such a classification is no easy task. The sheer size of the group has proved an effective deterrent (one in five lepidopteran genus-group names is noctuid; Nye, 1975), and its worldwide although primarily tropical distribution has resulted in there being few institutions where the work can be pursued on the required scale. Nevertheless, over the years, the genera of noctuids have been classified into tribes and subfamilies. Many of these taxonomic groupings, particularly the earlier ones, were inadequately characterised and this, together with differences of opinion, extensive synonymies at all levels and a dependence upon superficial characters, has led to a far from satisfactory situation.

This review is primarily historical and aims to trace and describe the development of the higher (i.e. suprageneric) classification of the noctuids from its earliest beginnings to the present day. The impact and use of the various authors' systems will be discussed, as will the characters upon which they were based (where these were reported). Finally, a provisional cladistic analysis is performed, using characters drawn from the literature. Each of the noctuid subfamilies is considered in turn, and its relationships assessed and conclusions reached as to where future research might be best directed.

Several conventions will be used subsequently and these are listed below.

1. No authors' names are used (if required, these can be found in Nye, 1975, and Watson *et al.*, 1980).
2. The generic, tribal and subfamilial names used will be those employed in the works discussed at that point in the review. If subsequent changes have been made, the most recently accepted name will be given in square brackets, immediately following the original, e.g. *Gonoptera* [*Scoliopteryx*]. Objective synonymies follow Nye (1975). Subjective synonymies generally follow Franclemont & Todd (1983) for North American taxa, Kloet & Hincks (1972) for British taxa and the BMNH card index for all other groups. Some subjective synonymies (e.g. *Heliothis/Helicoverpa*) may therefore not agree with the reader's opinions.
3. Where transfer of genera between subfamilies by other authors has been carried out, the name given in square brackets is the subfamily to which the genus was assigned by Nye (1975). Exceptions to this are: (*a*) the Agaristinae and Nolinae are treated here as subfamilies of the Noctuidae; and (*b*) the Acronictinae (s.str.) is separated from the Amphipyrinae.

In addition, the names Herminiinae, Hypenodinae and Rivulinae are not employed and it must therefore be realised that many genera that correctly belong in such subfamilies are treated as belonging to others (e.g. the Hypeninae s.l.).

In the beginning

Early days

Linnaeus (1758) divided the moths into two large genera, *Sphinx* and *Phalaena*. The latter was further divided into seven 'subgenera': *Bombyx, Noctua, Geometra, Tortrix, Pyralis, Tinea* and *Alucita*. Forty species of true noctuids were contained in the section of *Noctua* described as 'spirilingues, dorso cristato', together with the thyatirid, *Phalaena Noctua* [*Achylia*] *flavicornis*. However, due to Linnaeus' reliance upon superficial characters (e.g. degree of development of

the proboscis and the body vestiture), several noctuid species were placed in *Bombyx* (e.g. *B.* [*Scoliopteryx*] *libatrix, B.* [*Colocasia*] *coryli* and *B.* [*Dicycla*] *oo*).

The family Noctuidae was probably first recognised as a distinct unit by Denis & Schiffermüller (1775). Their division 'Noctuae' was divided into 21 groups, based on characters drawn from all developmental stages, including larval foodplants and habits. Each group was assigned a letter of the alphabet and accompanied by short diagnoses of the larvae and adults.

Many of the groups were very heterogeneous and some contained species no longer considered to be Noctuidae. Most of the remainder combined representatives from several current subfamilies. The hypenines were included in the Pyralides as group A, 'Phalaenae Pyralides Longipalpes'.

Up to the nineteenth century, classifications were still largely based upon local faunas. However, Borkhausen (1792) considered all the European noctuid species and divided them into two large groups, the *Noctuae fasciatae* and the *Noctuae non fasciatae*. These contained six and 20 families respectively. Although characters were drawn from the morphology and habits of several life-history stages, Borkhausen utilised only the wing patterns and resting positions of the adults and ignored all other structures. As a result, the classification was not particularly natural. For example, one group consisted of those species with yellow hindwings, from such genera as *Noctua, Anarta, Polyphaenis, Panemeria, Thalpophila* and various quadrifines. Nevertheless, this arrangement, albeit imperfect, was an improvement.

Hübner (1805) divided the noctuids into three sections (the Bombycoides, Genuinae and Semigeometrae), while Haworth (1803–28) regarded the family as consisting of only three genera: *Noctua, Phytometra* and *Hemigeometra*, subdivided into 22, three and two sections respectively.

This brief survey of the very early history of noctuid classification is by no means comprehensive. A more detailed review of this period (1720–1835) can be found in Guenée (1852–4: xlix–xc).

Guenée's first classification

In a paper of six parts, published between 1837 and 1841, Guenée presented the first detailed classification of the noctuids, which were variously referred to as the family Nocturni, the division Noctuae, or, most frequently, the Noctuélides. As such, this arrangement will be considered in more detail than its predecessors. Unfortunately, the system 'evolved' during the publication period, for reasons that were never stated, and this makes its description more difficult. Initially, Guenée listed 18 tribes. In addition, he also recognised the Noctuo-Bombycidae (Table 1). This last tribe mainly contained species of the family Thyatiridae, but also included three species of *Cosmia* [Amphipyrinae]. A fourth *Cosmia* species, *C. trapezina*, was excluded.

Of the remaining 18 tribes, only the first six were dealt with in the first part of the paper (Guenée, 1837) and so these are the only tribes for which his original concepts are known.

Although included in the 1837 list, Guenée discussed neither the Bombycoidi nor the Pseudo-Bombycidi, but begin with the third tribe, the monobasic Bryophyagidi. This contained only *Bryophila* [*Cryphia*], a genus that Guenée found difficult to place within the Noctuélides.

The Nonagridi consisted of two genera, *Nonagria* and *Gortyna*, the larvae of which are root- and stem-borers and, as such, show similar adaptations (smooth, supple integument; well-developed prothoracic and anal shields) which Guenée accepted as evidence of close relationship.

The Leucanidi comprised six genera, representing a mixture of noctuines, hadenines, acronictines and amphipyrines. They differed from the Nonagridi chiefly in that the larvae are leaf-feeders.

The last tribe dealt with by Guenée in 1837 was the Noctuelidi, consisting of seven genera, which are mostly Noctuinae but also including a few hadenines.

Guenée (1838*a*) continued his classification with the tribes Amphipyridi (four genera) and the Miselidi (three genera). The next tribe to be considered (Guenée, 1838*b*) was the Hadenidi. Ten

Table 1 A comparison of the tribes employed by Guenée in his 'Essai'. The Roman numerals given in the second column refer to the order in which the tribes were presented at the beginning of the work (Guenée, 1837), while the Arabic numbers given in the third column are those assigned to the tribes at the conclusion of the work (Guenée, 1841*b*).

TRIBE	1837 number	1841*b* number
Noctuo-Bombycidae	—	2 (as Noctuo-Bombycidi)
Bombycoidi	I	1
Pseudo-Bombycidi	II	—
Bryophagidi	III	3 (as Bryophagidae)
Nonagridi	IV	—
Leucanidi	V	4
Apamidi	—	5
Noctuelidi	VI	6
Amphipyridi	VII	13
Miselidi	VIII	—
Hadenidi	IX	8
Orthosidi	X	7
Xylinidi	XI	9
Heliothidi	XII	10
Ctenoceridi	XIII	—
Plusidi	XIV	11
Calpidi	—	12
Catocalidi	XV	15
Ophiusidi	XVI	14
Noctuoidi	XVII	16 (as Phalaenoidi)
Acontidi	—	17
Noctuo-Phalaenidi	XVIII	18

very diverse genera were included, from the Hadeninae, Cuculliinae, Amphipyrinae, Euteliinae, Ophiderinae and Thyatiridae. Guenée recognised the heterogeneous nature of both this and the next tribe (Orthosidi), accepting that they were almost completely artificial. Indeed, he found difficulty in devising good characters to separate them and even went so far as to label them both 'Tribu IX'. The Orthosidi itself was described in 1839 and contained elements of all four major trifine subfamilies.

The second tribe to be considered in 1839, the Xylinidi, was composed primarily of cuculliines but also included several hadenines and a single heliothine (*Chariclea* [*Periphanes*] *delphinii*). This last species was regarded as a link between the Xylinidi and Orthosidi, and the Heliothidi, the tribe that contained the remaining heliothines, together with the hadenine genus, *Anarta*.

The next tribe in Guenée's 1837 list was the Ctenoceridi. However, he must have reconsidered its validity, for its fails to appear in sequence (Guenée, 1841*a*). Instead, the Heliothidi were followed by the Plusidi, a tribe corresponding to the current Plusiinae. In contrast, the Calpidi, absent from the 1837 list, was included and contained only a single species, *Calpe* [*Calyptra*] *thalictri*. This tribe was followed by the Ophiusidi, a mixture of catocalines and ophiderines (e.g. *Lygephila* and *Minucia*), and the Catocalidi, which consisted only of *Catocala* and the ophiderine *Catephia*.

The final part of the *Essai* (Guenée, 1841*b*) considered three tribes. For the first, Guenée used the name 'Phalaenoidi' rather than Noctuioidi (as used in Guenée, 1837). This was because he thought the sole included genus, *Brephos* [*Archiearis*] had much in common with the Phalaenides [Geometridae] and formed a link between the two families. Guenée placed the genus within the Noctuélides because it was more similar to this family in all its life-history stages than to either the Geometridae or the Pyralidae.

The Acontidi and the Noctuo-Phalaenidi were similar in such characters as the form of the larvae, antennae and the relative width of the wings. The latter tribe was seen as the natural link between the Noctuélides and the Pyrales.

The final classification of the noctuids proposed by Guenée (1841*b*) (Table 1) contained a number of changes in both the names and contents of the tribes compared to those employed in previous parts of the paper. This was true even for that part with which the list appeared. The composition of the Bombycoidi was now stated as *Colocasia* [Pantheinae], *Acronicta* and *Moma* [Acronictinae], while the Pseudo-Bombycidi had either been omitted or merged with another tribe.

The next few tribes had undergone extensive modification and rearrangement. The two genera that formed the Nonagridi were separated, with *Nonagria* placed in the Leucanidi and *Gortyna* included in a new tribe, the Apamidi. Other apamid genera included *Glottula* [*Brithys*], *Xylophasia, Apamea* (removed from the Leucanidi) and *Mithymna* [sic] [now containing only [*Eriopygodes*] *imbecilla*, not originally included in the genus]. .

The Noctuelidi remained more or less intact, although it had gained *Rusina* from the Leucanidi. The Orthosidi gained *Scoliopteryx* from the Hadenidi, and *Tethea* [*Zenobia*] and *Cosmia* from the Noctuo-Bombycidi, together with several other changes, while the Miselidi were included within the Hadenidi. Otherwise this last tribe remained virtually unaltered, like most of the others. The only significant alteration to the Ophiusidi and the Catocalidi was the transfer of *Catephia* to the former tribe.

Alternatives to Guenée

Shortly afterwards, Duponchel (1844–6) constructed a classification of the Lepidoptera of Europe. He recognised only three families: the Diurnes (butterflies), Crepusculares (mainly sphingids) and Nocturnes. The noctuids comprised 24 tribes within the last of these (Table 2), corresponding largely to those of Guenée (1841*b*). There were, however, some notable differences.

Firstly, *Bryophila* [*Cryphia*] was included within the Bombycoides. With regard to the Nonagridi, Duponchel placed the genera *Gortyna* and *Hydroecia* [*Hydraecia*] in a separate

Table 2 The tribes employed by Duponchel (1844–6) for the noctuid moths, within his lepidopteran division, Nocturnes.

Number	Tribe
XVI	Bombycoides
XVII	Noctuo-Bombycides
XVIII	Orthosides
XIX	Gortynides
XX	Nonagrides
XXI	Leucanides
XXII	Caradrinides
XXIII	Apamides
XXIV	Hadenides
XXV	Noctuelides
XXVI	Amphipyrides
XXVII	Xylinides
XXVIII	Heliothides
XXIX	Calpides
XXX	Plusides
XXXI	Catocalides
XXXII	Ophiusides
XXXIII	Anthophilides
XXXIV	Agrophilides
XXXV	Anomalides
XXXVI	Phalenoides
XXXVII	Goniatides
XXXVIII	Acontides
XXXIX	Noctuo-Phalenides

tribe, the Gortynides, and *Nonagria* as the sole genus of the Nonagridi. The Apamides were thus equivalent to Guenée's 1841 Apamidi less *Gortyna* and *Hydraecia*, while the remaining genera of his 1841 Leucanidi were distributed between two tribes, the Leucanides and the Caradrinides.

Duponchel's second innovation was the division of the Noctuo-Phalaenidi into five tribes. The first, the Anthophilides, contained four acontiine genera while the Agrophilides included two. The latter tribe also included the amphipyrine *Metaponia*. A second amphipyrine genus (*Metoptria* [*Synthymia*]) was placed in the Goniatides, together with *Euclidia*, while two more amphipyrines (*Haemerosia* and *Erastria* [*Hapalotis*]), along with the acontiine *Oratoscelis* [*Calymma*] and the ophiderine *Phytometra*, constituted the Noctuo-Phalenides proper. The final tribe, the Anomalides, included a single species, *Timia* [*Axia*] *margarita*, which is currently placed in the Axiidae (Geometroidea). Thus, some of the heterogeneity of Guenée's Noctuo-Phalaenidi was removed by Duponchel, but not all.

In the following year, Herrich-Schäffer (1845) proposed a series of groupings of the moths he called the Noctuidae. He excluded the species hitherto placed in the Noctuo-Bombycidi, including them in a separate family, the Cymatophoridae [Thyatiridae]. Nevertheless, their position at the head of the Noctuidae suggests that Herrich-Schäffer still considered them to be intermediate between this family and the preceding Bombyces.

Two other families were associated with the Noctuidae. The first, the Nycteolidae, included genera presently placed in the Chloephorinae (*Chloephora, Earias*), Sarrothripinae (*Nycteola*), Ophiderinae (*Rivula*) and Hypeninae (*Schrankia* [*Hypenodes*]). The second family, the Brephidae, was equivalent to the Phalaenoidi.

The Noctuidae were divided into 24 subfamilies (Table 3). Herrich-Schäffer followed Duponchel in placing *Bryophila* [*Cryphia*] in the Bombycoidae [mainly Acronictinae]. He also included *Demas* [*Colocasia*] *coryli*, which Duponchel put in the Liparides [Lymantriidae] (although Guenée (1841*b*) placed it in the Bombycoidi), and *Diloba caeruleocephala*, previously

Table 3 Herrich-Schäffer's (1845) classification of the noctuid moths.

Tribe 1:	Cymatophoridae	
Tribe 2:	Noctuidae	
Subtribe	1:	Bombycoidae
	2:	Orthosidae
	3:	Hadenidae
	4:	Xylinidae
	5:	Cucullidae
	6:	Gonopteridae
	7:	Cerastides
	8:	Amphipyridae
	9:	Noctuidae
	10:	Heliothidae
	11:	Maniidae
	12:	Eriopidae
	13:	Eurhipidae
	14:	Calpidae
	15:	Herminidae
	16:	Metoponidae
	17:	Plusidae
	18:	Erastridae
	19:	Ophiusidae
	20:	Acontidae
	21:	Goniatidae
	22:	Hypenidae
	23:	Leptosidae
	24:	Aglenidae
Tribe 3:	Nycteolidae	
Tribe 4:	Brephidae	

included in the Notodontides since Linnaeus (1758). Finally, *Symira* [*Simyra*] was removed from its long-held relationship with the wainscots (*Leucania*) (some of which *Simyra* superficially resembles) and placed near *Acronicta*, its present position.

The next two subfamilies of Herrich-Schäffer, the Orthosidi and the Hadenidi, contained most of the remaining trifine noctuids less those placed in the Noctuidae, Xylinidae and Cuculliidae. *Mania* [*Mormo*] *maura* was removed from the Amphipyridi and included with *Placodes* [*Eucarta*] *amethystina* (from the Hadenidi) in the Maniidae. *Mania* [*Naenia*] *typica* was placed in the genus *Neuria* in the Hadenidae.

The Noctuidae, Heliothidae, Acontidae, Amphipyridae (less *Mania*), Plusidae and Calpidae were largely unchanged. Very small subfamilies were erected to accommodate *Hoporina* [*Jodia*] and *Cerastis* (Cerastides), *Eriopus* (Eriopides), *Eurhipia* [*Eutelia*] (Eurhipidae) and *Gonoptera* [*Scoliopteryx*] (Gonopteridae). New subfamilies of somewhat larger size were the Metoponidae, the Leptosidae and the Aglenidae. *Erastria* [*Hapalotis*] was removed from the Noctuo-Phalaenides of Duponchel and placed in a separate subfamily, the Erastridae.

The Ophiusidae comprised *Catephia* and *Ophiusa*, but because this last genus also included species currently assigned to such genera as *Lygephila*, the Ophiusidae was roughly equivalent to Guenée's (1841*b*) Catocalidi and Ophiusidi combined.

The most revolutionary aspect of Herrich-Schäffer's classification was his treatment of the deltoids. These were split into two subfamilies, the Herminidae and the Hypenidae (this also including several acontiines). The decision to include the deltoid genera *within* the Noctuidae was well ahead of its time and was only slowly to gain acceptance.

Guenée's second classification

The next major classification of the noctuids was that of Guenée (1852–4). The influence of Duponchel and Herrich-Schäffer was evident, for the arrangement proposed (Table 4) incorporated many of their groupings. This classification was to exert a significant influence on the ideas of future workers and thus is discussed in detail.

Two major divisions of noctuids were recognised, the Noctuélites and the Deltoïdes. Guenée removed this latter group from the Pyrales because he considered them to have more in common with the Noctuélites. However, despite the recognition that the two groups graded almost

Table 4 Guenée's second classification (1852–4) of the Noctuidae. Two 'divisions' were recognised, of which the former was split into two 'phalanges'. Each phalange was further divided into sections termed 'tribus', which are not equivalent concepts to the present category of tribe.

DIVISION: NOCTUÉLITES
PHALANGE: TRIFIDAE
TRIBU: 1 Bombyciformes
Family: 1 Noctuo-Bombycidae
2 Bryophilidae
3 Bombycoïdae
TRIBU: 2 Genuinae
Family: 1 Leucanidae
2 Glottulidae
3 Apamidae
Subfamily: 1 Gortynides
2 Xylophasides
3 Episémides
4 Apamides propres
4 Caradrinidae
5 Noctuidae
6 Orthosidae
7 Cosmidae
8 Hadenidae
9 Xylinidae
10 Heliothidae

Table 4 – *cont.*

TRIBU: 3 Minores
Family: 1 Haemerosidae
2 Acontidae
3 Erastridae
4 Anthophilidae
5 Phalaenoidae
PHALANGE: QUADRIFIDAE
TRIBU: 1 Sericiae
Family: 1 Palindidae
2 Dyopsidae
TRIBU: 2 Variegatae
Family: 1 Eriopidae
2 Eurhipidae
3 Placodidae
4 Plusidae
5 Calpidae
6 Hemiceridae
7 Hyblaeidae
8 Gonopteridae
TRIBU: 3 Intrusae
Family: 1 Amphipyridae
2 Toxocampidae
3 Stilbidae
TRIBU: 4 Extensae
Family: 1 Polydesmidae
2 Homopteridae
3 Hypogrammidae
Subfamily: 1 Yridae
2 Hypogrammidae propre
TRIBU: 5 Limbatae
Family: 1 Catephidae
2 Bolinidae
3 Hypocalidae
4 Catocalidae
5 Ophideridae
Subfamily: 1 Ophideridae propre
2 Phyllodidae
TRIBU: 6 Patulae
Family: 1 Erebidae
2 Ommatophoridae
3 Hypopyridae
4 Bendidae
Subfamily: 1 Hulodides
2 Bendides propres
TRIBU: 7 Serpentiae
Family: 1 Ophiusidae
2 Euclididae
3 Poaphilidae
4 Remigidae
TRIBU: 8 Pseudo-Deltoïdae
Family: 1 Focillidae
2 Amphigonidae
3 Thermesidae
DIVISION: DELTOÏDES
Family: 1 Platydidae
2 Hypenidae
3 Herminidae

imperceptibly into one another, Guenée did not regard this to be sufficient grounds for uniting them into a single division. Thus a graded sequence was identified, passing from the Bombyciformes (through which the Noctuélites were connected to the Bombyces) through to the Pseudo-Deltoïdae (by which the Noctuélites passed into the Deltoïdes and thence into the pyralids and geometrids).

Noctuélites. Within this division, Guenée recognised two large groups, which he termed 'phalanges', the Trifidae and the Quadrifidae. These were primarily separated on the now-infamous character of the degree of development and position of vein M_2 of the hindwing. In the Trifidae, this vein is generally much weaker than those following it, and originates at such a position that crossveins m_1–m_2 and m_2–m_3 are approximately equal in length. This gives the veins forming the posterior part of the discal cell a trifid appearance. In the Quadrifidae, M_2 is a strong vein originating near the posterior angle of the cell, resulting in the quadrifid configuration.

Trifidae. The Trifidae were divided into three tribes: the Bombyciformes, the Genuinae and the Minores. Distinctions were based largely upon the superficial appearance of the adults and the number of prolegs and hairiness of the larvae. It should be noted that Guenée's concept of a 'tribe' (or tribu), to which the family was subordinate, is not equivalent to current usage, in which the tribe is subordinate to the family.

Bombyciformes. The first tribe was split into three families. The Noctuo-Bombycidae [Thyatiridae] were envisaged as being intermediate between the Noctuélites and the bombycid family, Notodontides, while the Bombycoidae [Acronictinae, part] formed a link with the Liparidae [Lymantriidae]. Guenée considered substituting the name Acronyctidae for Bombycoidae but felt that to do so would obscure their relationship with the Bombyces, even though the term Acronyctidae would result in a more uniform nomenclature. The third family, the Bryophilidae (the Bryophagidae of Guenée, 1837), *did*, however, have its name changed for exactly this reason.

An advance upon the 1841 list, with regard to the Bombyciformes, was the unification of the previously widely scattered elements of the Thyatiridae (= Noctuo-Bombycidae): *Thyatira, Leptina* and *Cymatophora* [*Achlya*]. Guenée also followed Herrich-Schäffer (1845) by including *Simyra* in the Bombycoidae.

Genuinae. The Leucanidae, the first 'genuine' family, comprised those species collectively known as 'wainscots'. The adults are pale-coloured, with a simple striate pattern, and the larvae are either endophagous, boring in the stems and roots of grasses, sedges and other monocotyledonous plants, or living concealed by day and feeding by night on Poaceae. The larval habits formed the basis of two subdivisions. At present, the borers (Nonagrides) are placed in the Amphipyrinae, while the rest (Leucanides) are put in the Hadeninae.

The larvae of the Glottulidae also feed internally, but in bulbous plants. The family contained only four genera (e.g. *Glottula* [*Brithys*]) representing a heterogeneous assemblage of hadenines, amphipyrines and ophiderines.

The larvae of the next three families generally conceal themselves by day, emerging only after dark to feed, although a few (*Gortyna* spp.) are root-borers. The first, the Apamidae, shared characters of both the Noctuidae and the Hadenidae. Guenée recognised that the Apamidae were heterogeneous and possibly subject to future modification and division. In order to indicate this, he separated the species into four subfamilies: the Gortynides, the Xylinides, the Episémides and the 'Apamides propres'.

In his 1841 classification, Guenée united the next family, the Caradrinidae, with the Leucanidae because the latter included the genus *Simyra*, which he considered to be intermediate. However, in the present work, Guenée (1852–4) had removed *Simyra* to the Bombycoidae and this allowed him to reinstate the Caradrinidae as a separate family.

The fifth family, the Noctuidae, generally conformed to the current concept of the Noctuinae.

It consisted chiefly of three large genera: *Agrotis* (in the broadest sense), *Triphaena* [*Noctua*] and *Noctua* [*Amathes, Graphiphora, Diarsia*]. Members of the Noctuidae were characterised by holding their wings flat over the back at rest, one wing slightly overlapping the other, which distinguished them from the Leucanidae and Caradrinidae, in which the wings are held roof-wise.

Guenée found the Orthosidae very difficult to differentiate from both the Noctuidae and the Hadenidae. Biologically, many of the Orthosidae share the feature of autumn or early spring appearance as adults. The family consisted of a mixture of hadenines and cuculliines.

The Cosmidae was erected to accommodate a group of genera (e.g. *Dicycla, Cosmia*) that, in his *Essai*, Guenée had included in the Orthosidi and the Noctuo-Bombycidi, but that were now considered to be distantly related.

Like the Orthosidae, the Hadenidae proved very difficult to characterise. In larval features, the family approached the Apamidae and Xylinidae, whereas the adults resembled the Orthosidae. All the included genera are currently placed in either the Hadeninae or Cuculliinae, except for *Phlogophora*, which is an amphipyrine.

In contrast to the preceding families of the Genuinae, the larvae of the remaining two feed exposed on plants (with rare exceptions). The Xylinidae contained *Cucullia, Calocampa* [*Xylena*], *Xylina* [*Lithophane*] and their relatives, with several smaller amphipyrine genera and one, *Nystalea*, now placed in the Notodontidae. The Heliothidae was characterised additionally by diurnally-active adults. The only alteration from the Heliothidi of the *Essai* (Guenée, 1839) was the inclusion of *Chariclea* [*Periphanes*], a genus previously placed in the Xylinidi.

Minores. The last of the trifid tribes, the Minores, was divided into five families. All were characterised by the small size of the adult insects, which often resembled geometrids, pyralids or tortricids, similarities that were not contradicted, in Guenée's opinion, by the early stages. The Minores comprised a very mixed group of families, subdivided primarily on the basis of whether the adult abdomen was slender or stout.

Of the latter type, the Haemerosidae consisted of only two genera, *Haemerosia* (now placed in the Amphipyrinae) and *Lepidomys* (currently in the pyralid subfamily, Chrysauginae). The other family with stout bodies, the Acontidae, was relatively larger and contained seven genera.

The first of the slender-bodied families, the Erastridae, contained only four genera, mostly acontiines but with at least one amphipyrine (*Erastria* [*Elaphria*] *venustula*). Most species of the Anthophilidae could be distinguished from the Erastridae by the lack of a forewing areole. Those possessing this structure could only be separated with difficulty. Eleven genera were included within the Anthophilidae.

The final family of the Minores was the Phalaenoïdae [Archiearinae], which Guenée continued to retain in the Trifidae.

Quadrifidae. The second 'phalange' of noctuids recognised by Guenée was the Quadrifidae. Although this group of tribes was 'notablement différente' from the Trifidae, the separation was not absolute. Guenée found that placing the quadrifid families into a linear sequence was much more difficult than for the Trifidae. Although he attempted to delimit the families as naturally as possible, problems still arose, particularly in those groups that seemed to have closer affinities with certain trifid genera, for example, the Bolinidae and the Acontidae, and the Eurhipidae [Euteliinae] and certain hadenids. In contrast, several families were particularly well defined, notably the Catocalidae and the Plusidae.

The Quadrifidae was divided into eight tribes on the basis of the wing venation and pattern, general facies and the labial palps.

Sericiae. This tribe consisted of two small, tropical families, the Palindidae (*Palindia* [*Eulepidotis*] and *Homodes*) and the Dyopsidae (*Dyops* and *Dyomyx*). Both are currently placed in the Ophiderinae.

Variegatae. The second tribe was the largest in the Quadrifidae, comprising eight families.

The first of these, the Eriopidae, was small, containing only five genera. On the basis of larval characters, Guenée allied it closely with the next family, the Eurhipidae. However, he found it impossible to synonymise the two on the grounds of differences between the adults. The Eurhipidae itself formed a well-defined family, corresponding to the present Euteliinae.

Another family in which the constituent genera had, like those of the Eurhipidae, been placed in the Hadenidi was the Placodidae. Only two genera were included: *Placodes* [*Eucarta*; Amphipyrinae] and *Diastema* [Acontiinae].

The largest family of the Variegatae was the Plusidae. In addition to the two genera currently assigned to the subfamily Plusiinae (*Abrostola* and *Plusia* s.l.), three other genera were also included, *Basilodes, Thyria* and *Plusiodonta*. Through this last genus, Guenée noted that the Plusidae graded into the Calpidae. This family had been extended to include not only *Calpe* [*Calyptra*] but also *Oraesia, Gonodonta* and *Hapigia*. The last of these was considered to have a hepialid or notodontid aspect, but Guenée placed it in the Calpidae because of the development of the proboscis and the palps. However, present classifications place *Hapigia* in the Notodontidae and so it is not surprising that Guenée found that this genus formed a convenient link between the Calpidae and the Hemiceridae, another family containing current notodontids (*Hemiceras* and *Canodia*). Guenée commented on the resemblance between the larvae of *Hemiceras* and *Cerura* (Notodontidae) and concluded that despite the superficial similarity of the adult insects to noctuids, the genera of the Hemiceridae, and *Hemiceras* in particular, could belong elsewhere. The transfer of *Hemiceras* and *Hapigia* to the Notodontidae was effected by Druce (1887), while *Canodia* was moved by Schaus (1901). Of the three remaining hemicerid genera, two (*Arcyophora* and *Plusiodes* [*Westermannia*]) are presently assigned to the Chloephorinae while the third, *Achantodes*, (a genus Guenée described as having the overall appearance of a large species of *Chilo*) presently resides in the Pyralidae: Glaphyriinae.

The seventh family of the Variegatae was a group of moths whose relationships are still uncertain today. Until Guenée, the Hyblaeidae had been classified in such families as the Calpidae, Ophideridae or Gonopteridae. However, Guenée's general conclusion was that the group was of uncertain position within the Noctuélites. In present-day classifications, the two constituent genera are widely separated with *Phycodes* placed in the Glyphipterigidae. The development of the current location of *Hyblaea* will be discussed in greater detail below.

The last family in the Variegatae contained seven genera (e.g. *Gonoptera* [*Scoliopteryx*], characterised by angled wings.

Intrusae. The third quadrifid tribe Guenée termed the Intrusae. It was divided into three families on the basis of the general facies of the larvae and adults. The first of these, the Amphipyridae, contained four genera, the majority now being placed in the Trifinae (mainly Amphipyrinae), although *Barydia* has been transferred to the Notodontidae (Nye, 1975).

The Toxocampidae showed great similarity to the last family (in Guenée's opinion) and like it, was divided into two groups based upon the larvae. Five genera were included, all of which are currently assigned to the Ophiderinae. The final family, the Stilbidae, was composed of a single species, *Stilbia hybridata* [*anomala*]. Consideration of all characters led Guenée to conclude that, like *Brephos* [*Archiearis*], *Stilbia* was totally isolated within the Noctuélites. At present, *Stilbia* is an amphipyrine.

Extensae. Three families were recognised within this tribe on the basis of wing shape and size of the legs.

The first family, the Polydesmidae, comprised three genera (*Pantydia, Polydesma* and *Diatenes*) which had marked affinities with certain genera of the Intrusae, from which they could be distinguished by the wing venation. The Polydesmidae were seen as a link between the Amphipyridae and the Homopteridae. This latter family was established by Boisduval (1840) for several genera, the larvae of which resemble those of the Catocalidae.

The Hypogrammidae was considered to be somewhat heterogeneous and Guenée thought that it might eventually have to be split. In order to draw attention to this, he established two subfamilies, the Yridae and the 'Hypogrammidae propre'.

Limbatae. This tribe was another group Guenée considered might have to be split. It consisted of five families, of which the Catocalidae and the Ophiusidae were thought to perhaps warrant a separate tribe. They were believed to be related, through several genera, to the Patulae, and through the Catephidae to the Extensae.

The Catephidae and the Bolinidae were considered to have much in common. Seven genera comprised the former. Three (*Stictoptera, Odontodes* and *Lophoptera*) are currently assigned to the Stictopterinae, while of the other four, three are ophiderines, and one (*Cocytodes*) is a catocaline. There were only four genera in the Bolinidae: *Leucanitis, Panula, Bolina* [*Aleucanitis*] and *Syneda* [*Drasteria*], of which the first is presently a catocaline, the other three ophiderines.

The genus *Hypocala* was the sole component of the Hypocalidae and superficially resembled the hyblaeids. Guenée was uncertain as to its relationships, but on the basis of the form of the palps suggested a link with the Bolinidae.

Two genera, *Parthenos* [*Euparthenos*] and *Catocala*, were placed in the Catocalidae. Similarities in wing pattern suggested a relationship with the Hypocalidae and the Ophideridae. The latter family contained some species that showed similarities to the Calpidae and others that tended towards the Erebidae (Patulae) and the Ophiusidae (Serpentiae). Two subfamilies were recognised, the 'Ophideridae propre' and the Phyllodidae.

Patulae. All quadrifids that, despite their large size, presented an essentially phalaeniform (= geometriform) aspect, were placed in this tribe. Four families were recognised. The Erebidae was a large family of many genera that was difficult to define using absolute structural characters, although Guenée felt that the overall facies was unmistakeable. The Ommatophoridae was similarly well defined in general appearance due to the large eyespot on the forewings of most species. Guenée considered this family to be very natural, despite the aberrant wing venation of genera such as *Cyligramma* (the only quadrifid genus to lack an areole) and *Argiva* [*Erebus*, part] (in which the hindwing venation is much reduced in the males).

Like the last family, the Hypopyridae was considered to form a link between the Erebidae and the Ophiusidae (Serpentiae).

Within the Bendidae, Guenée recognised two distinct subfamilies. The Hulodides comprised species of the genera *Homaea* and *Hulodes*, which are South East Asian and resemble certain species of *Hypopyra*, while the 'Bendides propres', inhabiting the Americas, included *Itonia* and *Bendis* [*Lesmone*].

Serpentiae. The seventh tribe of the Quadrifidae principally contained species previously recognised under the name *Ophiusa*, a genus that until then had been rather vaguely defined. The tribe was divided into four families, an arrangement Guenée considered provisional at best, because he knew so few of the larvae.

By far the largest family in the tribe (and also in the Quadrifidae) was the Ophiusidae, comprising those species with elongate larval prolegs and large, impressive adults, with velvet-like, apically-pointed forewings. It included a mixture of catocalines and ophiderines.

The sole European representative of the Euclididae (*Euclidia* [*Euclidia* + *Callistege*] was once placed in the Noctuo-Phalaenidi. Duponchel (1844–6) had separated it into the Goniatides but Guenée rejected that name on the grounds that it was not based upon an included genus (but see his own Bombycoidae). The six included genera were distinguished from other groups primarily by a reduced number of larval prolegs (three pairs).

The larvae of the Poaphilidae, in contrast, were characterised by four pairs of prolegs, although the adults were similar to those of the Euclididae. Seven genera were included, of which four are currently catocalines and three ophiderines.

Distinguished primarily by the form of the hindleg in the males, which is clothed with dense hair arranged in a single compressed line on each surface, the Remigidae included genera that are presently placed in both the Catocalinae and Ophiderinae.

Pseudo-Deltoïdae. The last tribe in the Noctuélites graded almost imperceptibly into the division Deltoïdes, although the two groups could apparently be distinguished using certain characters of the head. Three families were recognised.

The Thermesidae were the largest and that which approached most closely in general facies the Deltoïdes. Certain genera also showed some resemblance to genera of the Remigidae, Ophiusidae and Bolinidae.

The other two families were characterised by features of the palps and body vestiture. The Focillidae was recognisable by the form of the last palpal segment and by the somewhat angled wings. It contained four genera of ophiderines. The three genera of the second family, the Amphigonidae, bore a superficial resemblance to *Gonoptera* [*Scoliopteryx*] *libatrix* and are now placed in the Ophiderinae.

Deltoïdes. The second great division of noctuid moths was termed the Deltoïdes. Guenée considered the distinction between the last listed Noctuélites (e.g. *Palyna*, now a hypenine) and the first deltoids to be very fine but the two groups could be distinguished. As was discussed above, such was not the opinion of Herrich-Schäffer (1845) but Guenée could not countenance such a decision.

The Deltoïdes were divided into three families that were not assigned to tribes. The Platydidae comprised only three genera: *Trigonia* [*Claterna*], *Macrodes* and *Platydia* [*Yidalpta*]. As if to confirm Guenée's opinion regarding the fine distinction between the Noctuélites and the Deltoïdes, these genera are currently classified in the Ophiderinae. He believed that the Platydidae were the most noctuid-like of the deltoids, although on the basis of palp, antenna, body, leg and wing characters they were unequivocally deltoids.

The Hypenidae were considered by Guenée to be intermediate between the other two families and to epitomise the concept of the Deltoïdes. Most of the Hypenidae are currently in the Hypeninae but *Rhodina, Madopa* [*Colobochyla*] and *Pterhemia* are ophiderines.

The Herminidae was the largest and most varied family of deltoids, and that which Guenée thought most closely approached the Pyrales. He also considered it to be the most interesting family because of the great diversity of structure found within it. Many genera have specialised structures on the antennae or eversible hair-pencils on the legs of the males, which have led one group to be termed the 'fan-foots'. Most of the herminid genera are presently classed as hypenines but two (*Cyclopteryx, Rivula*) are placed in the Ophiderinae.

This then was the second arrangement of the noctuids proposed by Guenée. It was followed by Stainton (1857), as well as by Walker (1856–8) in his influential, if controversial, list of specimens in the British Museum. Not all workers, however, accepted Guenée's classification so readily, and criticism was not long in coming.

The American alternative

The opening move

Packard (1869) described many morphological characters of the family Noctuidae that he considered to be of use in classification, drawn mostly from the head, thorax and wings. It was by far the most detailed comparative study conducted up to that time. Packard divided the Noctuidae into two subgroups, approximating Guenée's Trifidae and Quadrifidae. However, he criticised Guenée's use of venational characters and condemned the divisions of the Trifidae in particular, calling them 'trivial groups of genera'. Packard preferred characters such as the length and narrowness of the clypeus and the form of the antennae to those from the venation or palps. At least he felt this was true for the temperate noctuid fauna, but expressed no opinion regarding those from other areas.

Consequently, Packard removed both the Sericiae and Variegatae (less then Gonopteridae) to the Trifidae. This combined group he termed the Noctuinae, while the remainder of Guenée's quadrifids became the Catocalinae.

Development of Grote's classifications (1874–1890)

1874. In his list of North American noctuids, Grote (1874) employed Packard's two subfamilies. However, Grote also included the deltoids within the Noctuae and also associated two other groups with the family: the Noctuo-Phalaenidae [Archiearinae] and the Bombyciae [Thyatiridae]. He also agreed with Packard's opinions concerning Guenée's tribal and family groups and employed no subdivisions in the Noctuae.

These criticisms had little or no effect on English authors (e.g. Butler, 1881; Meldola, 1881; Moore, 1881; Pryer, 1883–5), who continued to follow Walker (1856–8) and hence remained faithful to Guenée.

1882. A brief resumé of the classification of the noctuids was provided by Grote (1882*a*). He disagreed with Lederer (1857), who had removed the Cymatophoriden [Thyatiridae] and Brephiden [Archiearinae] from the Noctuidae and established them as separate families, and chose to include the Cymatophorina [Thyatiridae] and Brephina [Archiearinae] within the Noctuae. This was followed by the *New check list* (Grote, 1882*b*), in which the noctuids were subdivided although no reasoning was given.

Two major groups were recognised in the Noctuae: the Bombyciae [Thyatiridae] and the Noctuelitae (Table 5).

Within the latter, two subgroups were recognised, the Nonfasciatae and the Fasciatae

Table 5 The classification of the Noctuidae employed by Grote (1882*b*).

NOCTUAE
- Bombyciae
- Noctuelitae
  - (Non-Fasciatae)
    - Dicopinae
    - Bombycoidea
    - Noctuinae
    - Hadeninae
    - Nonagriinae
    - Pyrophilinae
    - Taeniocampinae
    - Orthosiinae
    - Cuculliinae
    - Nolaphaninae
    - Anomiinae
    - Litoprosopinae
    - Euteliinae
    - Ingurinae
    - Calpinae
    - Plusiinae
    - Stiriinae
    - Heliothinae
    - Eustrotiinae
    - Hyblaeinae
    - Noctuo-Phalaenidi
  - (Fasciatae)
    - Catocalinae
    - Ophiderinae
    - Toxocampinae
    - Erebiinae
    - Brotiinae
    - Pangraptinae
    - Deltoides
    - Hypeninae

(Packard's Noctuinae and Catocalinae), which were further divided into 21 and eight subfamilies respectively. Many of the groups employed by Grote corresponded to Guenée's families but, because the *New check list* was the first to subdivide the American noctuid fauna, Grote found it necessary to erect a number of new subfamilies, which can be summarised as follows:

Dicopinae: *Eutolype, Dicopis* [*Psaphida*, part], *Copipanolis* [Cuculliinae];
Pyrophilinae: *Pyrophila* [*Amphipyra*], *Caradrina* [e.g. *Athetis*] [Amphipyrinae];
Nolaphaninae: *Adipsophanes* [*Catabena*], *Crambodes, Nolaphana* [*Balsa*] [Amphipyrinae];
Anomiinae: *Anomis, Aletia* [*Anomis*], *Pteraetholix* [*Amyna*], *Chytoryza* [*Illatia*] [the first two are ophiderines; the third an acontiine; and the last an amphipyrine];
Litoprosopinae: *Litoprosopus* [Ophiderinae];
Ingurinae: *Ingura* [*Paectes*] [Euteliinae];
Stiriinae: *Stilbadium, Stiria, Acopa, Fala, Plagiomimicus* [Amphipyrinae];
Brotiinae: *Brotis* [*Sphacelodes*] *vulneraria* [Geometridae: Ennomiinae];
Pangraptinae: *Syllectra, Pangrapta, Phalaenostola* [the first two are now ophiderines, the last a hypenine].

In addition, several genera were moved between subfamilies. For example, the Plusiinae now included *Anarta* [*Anarta, Sympistis, Hada*], *Telesilla* [*Eucarta*] and *Lepipolys*. The deltoid genera were divided into two groups. The first, the Deltoides, contained many hypenine genera and some ophiderines (e.g. *Rivula*) while the second, the Hypeninae, consisted of *Hypena* and its relatives. The deltoids were classified within the Noctuelitae but, unlike Herrich-Schäffer (1845), Grote kept the two subgroups together at the end of the list.

In the same year, Smith (1882–3) published a synopsis in which he explicitly stated the characters used at each level of subdivision of the Noctuidae. He recognised three primary divisions characterised by the eyes being naked, hairy or lashed. Finer divisions were based upon tibial armature, clypeal modifications and the palps. However, Smith did not attach any formal names to his groups. Indeed, he considered *these divisions [to be] entirely artificial and the sequence of genera in the synopsis is not that to be followed in the systematic arrangement of the group, the object being only to enable the collector to place any unknown Noctuid into its proper genus with but little trouble.*

1883. The next year, Grote (1883) considered in more detail the structural characters he had used in his previous works. He reverted to Lederer's (1857) three families, in that the Noctuo-Phalaenidae were elevated to family status (as Brephidae). Also, the Bombyciae of Grote (1882*b*) was renamed the Thyatiridae (Cymatophoridae being inapplicable for reasons given in Harvey, 1874).

The Noctuidae themselves were divided as before but only the nonfasciate subfamilies were discussed in detail. Most were unaltered from the *New check list* but several changes had been made. For consistency, the Bombycoidea were renamed the Apatelinae, while the Euteliinae and Pyrophilinae became the Eurhipinae and Caradrinae respectively. The Bryophilinae (*Bryophila* [*Cryphia*] and its relatives) were split from the Apatelinae, while four genera (*Trichotarache* [*Acontia*, part], *Tarache* [*Acontia*, part], *Chamyris* [*Cerma*] and *Xanthodes* [*Bagisara*]) were removed from the Eustrotiinae as the Acontiinae.

Two new subfamilies were erected. The Arzaminae, comprising *Sphida* and *Arzama* [both *Bellura*] (previously placed in the Nonagriinae), and the Scolecocampinae, containing *Scolecocampa, Eucalyptera* [*Gabara*, part], *Cilla* [*Gabara*, part], *Amolita, Doryodes* and *Phiprosopus* [*Phyprosopus*].

1886. Meyrick (1886) was the first English author to adopt the characters advocated by Grote. However, Meyrick also employed Guenée's major divisions (based upon the development of hindwing vein M_2), calling them the Noctuidae and Plusiadae. No further subordinate groups were used.

1890. A revised checklist of North American noctuids was published by Grote in 1890. Two subfamilies were considered, the Thyatirinae and the Noctuinae (relegated from the rank of family). The latter was divided into 25 tribes. Most of these corresponded to those of Grote's previous works but there were discrepancies.

Arsilonche [*Simyra*] and *Raphia* were separated from the Apatelinae and, together with *Demas* [*Colocasia*], comprised the Bombycoidi. Not only was this name potentially confusing (cf the Bombycoidae of Guenée, 1852–4) but it was not based upon the name of an included genus and therefore ran counter to Grote's (1883) previous assertions regarding the correct formation of suprageneric names.

In addition, the Noctuinae were renamed the Agrotini, and the Eurhipidae reverted to the Euteliini, with the Ingurinae being included within it. New tribes were formed for *Lithophane, Calocampa* [*Xylena*], *Lithomia* [*Lithomoia*] and *Xylomiges* [*Egira*] (Calocampini); and *Cleophana* [*Copicucullia*] (Cleophanini). The Tarachinae lost *Trichotarache* [*Acontia*, part] to the Heliothini, while interposed between the former tribe and the Eustrotiinae was the new monobasic Cerathosiini (*Cerathosia tricolor*). This species had been described as an arctiid by Smith, near *Utetheisa*, but on the basis of wing venation and clypeal ornamentation, Grote felt certain that it was actually a noctuid. *Cerathosia* currently resides in the Acontiinae.

Grote (1890) gave only an outline of his classification of the rest of the family. More details were given in another paper (Grote, 1889–90). The Catocalinae were divided into two tribes. The Catocalini were characterised by their often brightly-coloured hind-wings and included the *New check list* subfamilies Catocalinae, Ophiderinae and Toxocampinae. The second tribe, the Pheocymini, comprised the Erebinae of the *New check list*. The wings of the included genera were generally concolorous and crossed by sinuous lines. Grote was unwilling to assign the remaining catocaline subfamilies of the *New check list*, the Brotiinae and the Pangraptinae, preferring to await a more thorough study of the Neotropical fauna.

Two tribes were recognised in the Deltoidinae. The herminiines could be distinguished by their concolorous wings, marked with continuous lines. The Hypenini, in contrast, had unicolorous hindwings while the forewings displayed the usual noctuid markings, albeit subdued.

The fourth subfamily of the Noctuidae, the Brephinae, now contained two genera, *Brephos* [*Archiearis*] and *Leucobrephos*. Grote recognised certain resemblances to some Geometridae (hairy abdomen, predominantly diurnal flight period, larvae with five pairs of prolegs [!] and similar habits) but still retained them in the Noctuidae.

Thus, by 1890, there were two competing, if somewhat internally unstable and inconsistent, systems for the classification of the Noctuidae. The first, based upon the work of Guenée, was widely accepted in Europe; the second, arising from the studies of Grote, was the primary system in use in North America. The stage was set for a comparative assessment.

Classifications in conflict

Tutt's comparison

After consideration of the available options, Tutt (1891–2) decided to adopt the system of Guenée, not because he thought it was more correct but because it was based upon characters of the early stages as well as the adult insect. Grote's system relied entirely on adult features. Only the points of contention as seen by Tutt will be discussed further.

Trifidae: Bombyciformes. Tutt considered as irrelevant the debate as to whether the Cymatophoridae [Thyatiridae] were to be placed as the last tribe in the Bombyces (Staudinger & Wocke, 1871) or as the first in the Noctuae (Guenée, Grote). He did explicitly note, however, that the eggs were of the geometrid type, and that the removal of the Cymatophoridae from the Noctuae would render the latter group more homogeneous.

Tutt concluded most authors to be in agreement over retaining the Bombycoidae (= Apatelini) and Bryophilidae in the Noctuae although Butler (1879) had dispersed the British

species of *Acronycta* [*Acronicta*] amongst the Arctiidae, Liparidae [Lymantriidae], Notodontidae and Noctuae (a position he later rescinded; Butler, 1893). Tutt also agreed with Staudinger & Wocke's (1871) inclusion of *Moma orion* [*alpinum*] in the Bombycoidae but expressed doubts regarding *Demas* [*Colocasia*] *coryli* and *Diloba caeruleocephala*, which he thought might belong elsewhere. He also rejected Grote's Bombycoidi on the grounds that Chapman (1893*a*) had demonstrated *Arsilonche* [*Simyra*] *albovenosa* [*venosa*] to be congeneric with *Acronycta* [*Acronicta*] *rumicis* and so *Arsilonche henrici* (the American species) could not therefore be placed in a separate tribe to the genus *Acronycta* [*Acronicta*].

Trifidae: Genuinae. Tutt considered this group to be far more natural, although he had reservations concerning the arrangements and contents of some of the families. He felt that, on the basis of larval habits and mode of pupation, Staudinger & Wocke's (1871) placing of the Gonopteridae in the Trifidae was correct. Tutt also believed that *Mania* [*Mormo* + *Naenia*] and *Amphipyra* might be better placed in the Trifidae, but that the Plusidae should remain in the Quadrifidae. This last point was the major difference between Guenée's Genuinae and Grote's Noctuinae.

Trifidae: Minores. Tutt acknowledged the anomalous nature of the Phalaenoidae (Brephidae) but retained it in the Trifidae. He considered Meyrick's (1892) transfer of this group to the Geometrina (as Monocteniadae) erroneous because the larvae have five pairs of prolegs (even though those on abdominal segments 3, 4 and 5 are reduced).

Quadrifidae: Limbatae. Tutt disagreed with Grote's suggestion that the Ophiderinae belonged in the Catocalini, considering that association to be based upon superficial characters. He also believed that the Toxocampinae, allied with the Catocalinae by Grote (1890), were nearer the Deltoides, a position about which 'there can be no doubt' when the larvae are examined.

Quadrifidae: Intrusae. This was the subclass about which Tutt had most doubts, especially when just the British representatives of the three families (Amphipyridae, Stilbidae and Toxocampidae) were examined. He did not believe that *Mania* [*Mormo*] and *Naenia* belonged in the Hadenidae (where they had been placed by Staudinger & Wocke, 1871) although he was reasonably satisfied with the position of *Amphipyra* in the Caradrinidae. Tutt also refused to accept *Aventia* [*Laspeyria*] *flexuosa* and *Boletobia* [*Parascotia*] *fuliginaria* ('an admitted geometer' – now an ophiderine) in the Noctuae, and thought the Stilbidae were sufficiently isolated to require special treatment, similar to the Brephides.

Deltoides. Tutt agreed with those who placed this group as an integral part of the Noctuae, and concurred with Grote's division of the subclass into the Herminiidae and Hypenidae, groups that Tutt considered to be very natural.

Overall, Tutt's general conclusions supported Guenée's classification, but with the following suggestions.

1. *Demas* [*Colocasia*] and *Diloba* were not Noctuae.
2. The Bryophilidae had no close relationship with the Bombycoidae.
3. The Leucanidae was unnatural, *Leucania* belonged in the Noctuidae and the Nonagriae in the Apamidae.
4. The Hadenidae and Apamidae were essentially identical.
5. The Xylinidae should be divided, because *Xylina* [*Lithophane*] and *Calocampa*]*Xylena*] were not closely related.
6. The Amphipyridae should be divided, with *Mania* [*Mormo*] and *Naenia* being placed in the Noctuidae and *Amphipyra* near the Caradrinidae.
7. The Plusidae were less closely related to the Xylinidae than were the Heliothidae.
8. The Toxocampidae were closer to the Deltoides than to the Catocalidae.
9. The Deltoides were unequivocally noctuids.

Smith's comparison

Smith (1891) held altogether different views. The Noctuina included three families: the Thyatiridae, the Noctuidae and the Brephidae. No subdivision was used because Smith considered Grote's subfamilies to be of no use because of their 'unequal value and impossibility of accurate definition'. Guenée's classification was not even considered. Smith's position had not altered two years later (Smith, 1893).

Hampson's Fauna of British India

The next major work on the higher classification of the Noctuidae introduced a new name but one which was to have a considerable impact in future years. The first arrangement of noctuid genera proposed by Hampson (1893–5) pioneered an entirely novel approach to family level interrelationships. Hampson believed that the three families Agaristidae, Arctiidae and Noctuidae were very closely related and difficult to separate clearly in some instances. In particular, he thought that the 'primitive' forms of the last two families (the Nolinae and Sarrothripinae respectively) graded into each other somewhat. The Nolinae were later considered to be worthy of a separate family, based upon larval characters (Packard, 1895).

Also included within the Arctiidae, as the subfamily Nycteolinae, were nine genera currently referable to the noctuid subfamily Chloephorinae. This group of genera had always been enigmatic and had generally been placed in the Bombyces as a separate family (e.g. Smith, 1891). Hampson (1893–5) noted that they approached the Acontiinae in the structure of the hindwing vein $Sc + R_1$ but on the basis of their 'tree-frequenting habits', retained them in the Arctiidae.

Table 6 The first classification of the Noctuidae proposed by Hampson (1893–5).

NOCTUIDAE
Trifinae
Acontiinae
Palindidae
Sarrothripinae
Euteliinae
Stictopterinae
Gonopterinae
Quadrifinae
Focillinae
Deltoidinae

The Noctuidae were divided into 10 subfamilies (Table 6). Two (the Acontiinae and the Trifinae) were characterised by an obsolete hindwing vein M_2, while in the other eight this vein was well developed. Hampson thus used Guenée's major subdivisions rather than Packard's.

The Agaristidae [Noctuidae: Agaristinae] were considered to be a development from the Noctuidae, the first occasion on which such a relationship had been postulated. Previously, they had been considered to be near the Arctiidae and in the Bombyces (e.g. Smith, 1891).

Trifinae. This subfamily approximated Guenée's Genuinae and was defined primarily on the basis of wing venation (as were many of Hampson's categories). It contained those genera presently referable to the Noctuinae, Heliothinae, Hadeninae, Cuculliinae and Amphipyrinae. The Trifinae also included *Acronycta* [*Acronicta*], but not the bryophilines (see below), and also *Toxocampa* [*Lygephila*], a view almost diametrically opposed to that held by Tutt (1891–2; 1902).

Acontiinae. This subfamily was distinguished from the last by the presence of a *slender* vein M_2 in the hindwing. The larvae generally have four pairs of prolegs but reduction of those on

abdominal segments 3 and 4 occurs in some species. Most of the 29 genera are still acontiines, but the subfamily also included two acronictines (*Diphthera* [*Moma*] and *Bryophila* [*Cryphia*]); three amphipyrines (*Megalodes, Cosmia* and *Pachylepis*); two ophiderines (*Rivula* and *Tathodelta*) and a hypenine (*Perciana*).

Palindiinae. Ten genera were included in this, the first of the quadrifine groups, representing a mixture of ophiderines and chloephorines, with one sarrothripine (*Bryophilopsis*) and one amphipyrine (*Callyna*).

Sarrothripinae. Seventeen genera constituted this subfamily. The majority are still sarrothripines, although *Ariola* is a chloephorine, *Nolasena* an ophiderine and *Chlumetia* a euteliine. Also included was the genus *Hyblaea*. None of the defining characters of this subfamily was constant but most had raised scales on the wings and a bar-shaped retinaculum in the male.

Euteliinae. Only three genera were included in this subfamily (*Ingura* [*Paectes*], *Anuga* and *Eutelia*) and all three presently reside here.

Stictopterinae. This was another very small subfamily, of seven genera. Apart from venational characters, the constituent genera also had fairly well-developed scale tufts on the forewing and frequently a hyaline area at the base of the hindwing. Only four of the genera are still stictopterines (*Stictoptera, Odontodes, Sadarsa* and *Gyrtona*). The others comprised a chloephorine (*Maceda*), an ophiderine (*Cymatophoropsis*) and a sarrothripine (*Risoba*).

Gonopterinae. Eighteen genera comprised this subfamily. Again, characterisation was vague, with most of the characters also occurring in some genera of other subfamilies. Seven of the 18 genera listed are now ophiderines, the remainder being chloephorines.

Quadrifinae. This subfamily was by far the largest in the Noctuidae, comprising 81 genera in all. Most are now placed in the Catocalinae or Ophiderinae but the subfamily also included genera assigned to the Plusiinae (*Plusia, Abrostola*), Amphipyrinae (*Cetola*), Pantheinae (*Moma* [*Trichosea*], *Trisuloides*) and Chloephorinae (*Pseudocalpe* [*Arcyophora*]).

Focillinae. In common with many genera of the previous subfamily, the larvae of the Focillinae are semi-loopers. The legs of the adults are also modified, possessing short, stout tibiae and tarsi. Thirteen genera were included, all ophiderines.

Deltoidinae. This group was relatively variable regarding wing venation and showed considerable complexity in male secondary sexual characters. Hampson considered groups such as the Trifinae, Acontiinae, Focillinae and Quadrifinae to have arisen from this subfamily.

The Deltoidinae contained 40 mainly ophiderine and hypenine genera but also two acontiines, *Araeopterum* [*Araeopteron*] and *Niaccaba*.

The Archiearinae are absent from India and were therefore not considered by Hampson. The Cymatophoridae [Thyatiridae] comprised a separate family, placed near the Notodontidae and the Sesiidae [Aegeriidae]. Although not placed near the Noctuidae, Hampson stated that were he to arrange the moth families in a linear sequence, then the Cymatophoridae would *follow* the Noctuidae, rather than precede them as had been more or less standard practice in the past. This was because he considered them to be a side-branch from the main stem leading from the tortricids, through the noctuids and notodontids, and thence to the Bombycoidea and Geometroidea (Fig. 1). As can also be seen from Fig. 1, Hampson dismissed a direct link between the noctuids and either the pyralids or the geometrids.

Further development of Grote's classification

In the meantime, Grote had been reappraising his noctuid classification. On the basis of

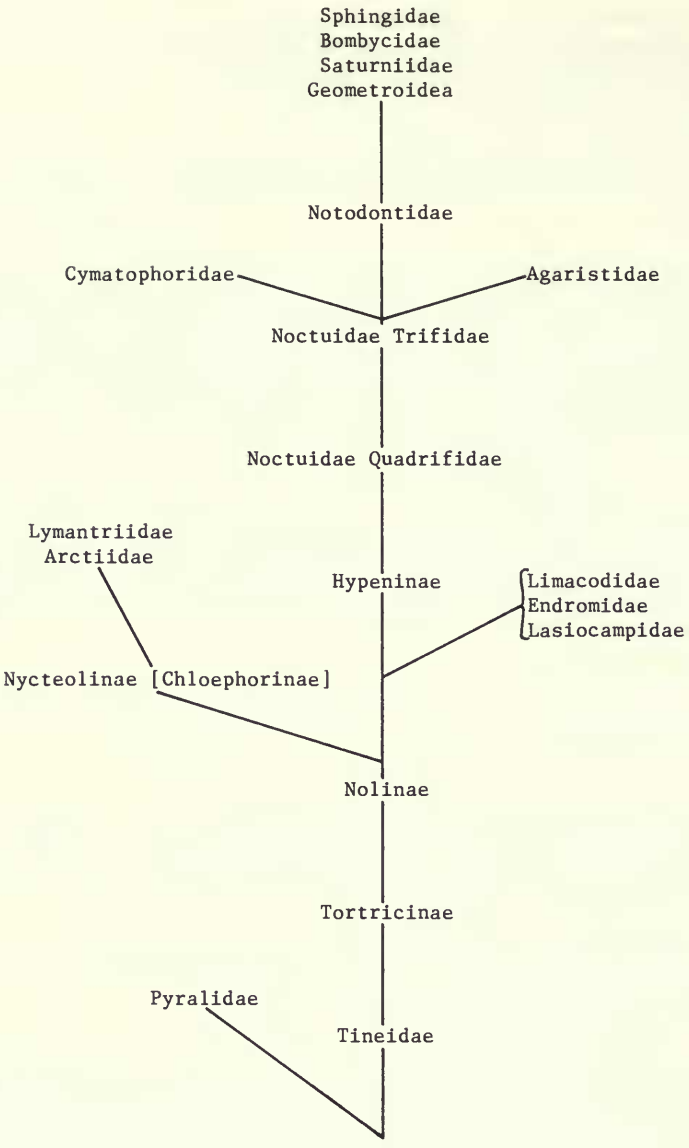

Fig. 1 Phylogeny of the higher Lepidoptera, with particular reference to the Noctuidae, proposed by Hampson (1893–5). Note that the Noctuidae are placed internally on the main stem leading from the tortricines to the geometroids and sphingids, while the arctiids form the terminus of a side-branch that splits off from the main stem below the noctuids.

[unstated] larval characters, he elevated part of the Apatelini to family status (Grote, 1895*a*) but continued to place them at the head of the Noctuidae. The Apatelidae, in addition to *Acronicta* and its relatives, also included *Leptina* [*Baileya*] (a sarrothripine), *Raphia* (an ophiderine), three pantheines (*Demas* [*Colocasia*], *Panthea* and *Charadra*) and three cuculliines (*Feralia, Arthrochlora* [*Feralia*] and *Momaphana* [*Momophana*]).

The Noctuidae became the Agrotidae on the grounds that the name *Noctua* was preoccupied in the birds. This began a long argument as to the correct family-group name for the noctuids. The subfamilies Catocalinae and Deltoidinae were not discussed in this paper (Grote, 1895*a*) but the remaining group (= Noctuinae) was divided into 24 tribes (Table 7), as follows.

Table 7 The classification of the Agrotidae [Noctuidae] followed by Grote (1895*a, b*). The first publication dealt with the tribes up to and including the Hyblaeini, the second considered the subfamily Catocalinae.

THYATIRIDAE
APATELIDAE
AGROTIDAE
- Agrotinae
  - Jaspidiini
  - Agrotini
  - Psaphidini
  - Hadenini
  - Bellurini
  - Nonagriini
  - Heliophilini
  - Scolecocampini
  - Balsini
  - Caradrinini
  - Orthosiini
  - Cleophanini
  - Cuculliini
  - Euteliini
  - Anomiini
  - Litoprosopini
  - Plusiini
  - Calpini
  - Stiriini
  - Heliothini
  - Acontiini
  - Cerathosiini
  - Eustrotiini
  - Hyblaeini
- Catocalinae
  - Euclidiini
  - Melipotini
  - Eulepidotini
  - Stictopterini
  - Ascalaphini
  - Catocalini
  - Ophiderini
  - Toxocampini
  - Thysaniini
  - Pheocymini
  - Pangraptini
  - Hexerini
  - Boletobiini

Jaspidiini. This tribe of seven genera (the Bryophilinae of Grote, 1883) had been excluded from the Apatelidae when this was raised to family rank. The name was based upon *Jaspidia* Hübner [1806], which Grote (1895*a*) had substituted for *Bryophila* Treitschke 1825.

Agrotini. The large genus *Agrotis* and four smaller genera (*Anytus* [*Sutyna*], *Richia, Eucoptocnemis, Agrotiphila*) constituted this tribe, which thus approximated the Agrotini of Grote (1890). The following were transferred out: *Adita* (Hadenidi), *Copablepharon* (Heliothini), *Ufeus* and *Pteroscia* [*Anomogyna*] (both Heliophilini).

Psaphidini. This was the Dicopini of Grote (1890).

Hadenini. Equivalent to the Hadenini of Grote (1890), the genera of this tribe had undergone considerable rearrangement and renaming.

Bellurini. This was the Arzamini of Grote (1890).

Nonagriini. This tribe now contained only the first five genera (*Nonagria – Tapinostola*) of the tribe of the same name in Grote (1890).

Heliophilini. The remaining three nonagriines (*Ommatostola, Heliophila* [*Mythimna*] and *Zosteropoda*), together with *Ufeus* and *Pteroscia* [*Anomogyna*], constituted this new tribe.

Scolecocampini. There had been no change from the Scolecocampini of Grote (1890).

Balsini. This was the Nolaphanini of Grote (1890).

Caradrinini. This tribe was essentially unchanged from the Caradrini of Grote (1890). However, *Monodes* [*Elaphria*] had been transferred to the Nonagriini (and sunk to *Platysenta*).

Orthosiini. This tribe was equivalent to the combination of the Orthosiini and Calocampini of Grote (1890).

The remaining 13 tribes were unchanged from Grote (1890) although the Tarachini had been renamed the Acontiini and lost *Trileuca* [*Schinia*, part] to the Orthosiini.

Smith on the deltoids

Smith (1895), in his revision of the deltoids, recognised this group of moths to be devoid of exclusive defining characters, although the general facies was relatively distinctive. As restricted by him, Smith considered that the group might merit subfamily rank within the noctuids. However, he refrained from formally proposing such a grouping. Three (to Smith) very distinct tribes were included: the Heliini (*Epizeuxis* only), the Herminiini and the Hypenini. Two genera were excluded, *Pseudorgyia* and *Rivula*, both of which are now considered as ophiderines. Smith also felt that the assignment of the latter to the Nycteolidae [Sarrothripinae] might not have been the error most previous workers had considered it to be.

Grote on the deltoids (and other noctuid groups)

Grote (1895*b*) considered that no stable classification could ever be achieved for the Noctuidae until the North American and European faunas were studied together. In a paper written as a conclusion to that of 1883, many of his ideas concerning noctuid classification were expanded and reinterpreted.

The Thyatiridae were omitted, support being drawn from Dyar's work on larvae, which showed the group to be structurally related to the Geometridae and Platypterigidae [Drepanidae]. The noctuid moths, therefore, consisted of three families, the Apatelidae, Agrotidae and Brephidae.

Agrotidae: Agrotinae. *Harrisimemna* was removed from the Jaspidiini and placed in the Apatelidae, while *Raphia* was moved from the latter group to the Hadenini. Grote postulated a relationship between *Raphia* and *Episema* [*Diloba*] although he had not examined the European species of those genera.

The Calocampini was resurrected but only contained *Lithomia* [*Lithomoia*] and *Calocampa* [*Xylena*]. *Lithophane* remained in the Orthosiini.

Pyrophila [*Amphipyra*] was removed to a monobasic tribe, the Pyrophilini. Grote agreed with Smith's placement of *Pseudorgyia* in the Scolecocampini, but having failed to find a satisfactory position for *Rivula* (he could not place it in either the Nycteolidae [Sarrothripinae] or the Pseudoipsidae [Chloephorinae]), Grote was forced to erect a new tribe to receive it, the Rivulini.

Agrotidae: Catocalinae. Thirteen tribes were recognised in this subfamily (Table 7).

Euclidiini: a mixture of eleven genera of catocalines and ophiderines (e.g. *Parallelia, Drasteria, Phurys* [*Ptichodis*], *Poaphila* [*Argyrostrotis*]).

Melipotini: Grote included six genera in this tribe (e.g. *Hypocala, Melipotes* [*Bolina*]), all of which are now ophiderines. He considered the distinction between this tribe and the last to be difficult.

Eulepidotini: *Eulepidotis* and *Palindia* [*Eulepidotis*] [Ophiderinae].

Stictopterini: *Stictoptera* and *Magusa* (the latter now an amphipyrine).

Ascalaphini: ten genera constituted this tribe, of which most are now ophiderines but *Remigia* is a catocaline, *Argillophora* an acontiine and *Fagitana* an amphipyrine.

Catocalini: *Allotria, Andrewsia* [*Catocala*, part] and *Catocala* [Catocalinae].

Ophiderini: *Ophideres* [Ophiderinae] and *Euparthenos* [Catocalinae].

Toxocampini: *Toxocampa* [*Lygephila*] and *Eutoreuma* [*Isogona*] [Ophiderinae].

Thysaniini: *Erebus* [*Ascalapha*] [Catocalinae], *Thysania* and *Letis* [Ophiderinae].

Pheocymini: this tribe was relatively large, containing 12 genera (e.g. *Zale, Yrias* [*Metria*]), of which four are now placed in the Ophiderinae and the remainder in the Catocalinae.

Pangraptini: *Phalaenostola* [Hypeninae], *Zethes, Syllectra* and *Pangrapta* [Ophiderinae].

Hexerini: this tribe contained only *Hexeris* [*Triprora*], now classified in the family Thyrididae.

Boletobiini: of the four included genera, two (*Boletobia* [*Parascotia*] and *Aventia* [*Laspeyria*] are ophiderines, *Acherdoa* is an amphipyrine and *Dyaria* [*Coenodomus*] is placed in the pyralid subfamily Epipaschiinae.

Agrotidae: Hypeninae. Grote considered the subfamily name, Deltoidinae, which he had proposed himself in 1890, to be objectionable because it was not based upon any included genus. He thus substituted Hypeninae. Two of Smith's three tribes were retained, the Heliini being considered insufficiently distinct from the Herminiini to warrant separate status.

The position of *Nycteola*

The nycteolines had originally been placed among the tortricids but by the late nineteenth century were generally included in the Bombyces as a separate family, most commonly known as the Nycteolidae (e.g. Smith, 1891). Frequently, a group of genera including *Earias* and *Pseudoips* was also included, but more often these genera were placed in a distinct though related family, the Pseudoipsidae.

Nycteola had also been referred to the Noctuidae but as a deltoid. Grote (1895*b*) disagreed with this. Examination of the immature stages revealed similarities to *Pseudoips* [*Bena*] *bicolorana* [*prasinana*] but peculiarities in the wing shape and venation led Grote to believe that *Nycteola* did not belong in either the Pseudoipsidae [Noctuidae: Chloephorinae] (which Grote recognised as distinct) or the Noctuidae.

A study of the larval chaetotaxy of *Nycteola* by Dyar, which was communicated by Grote, bore out the latter's opinions regarding the close relationship between this genus and the Pseudoipsidae, and even suggested that the two groups might not be distinct. However, Grote retained the family rank of the Nycteolidae.

Hampson (1893–5) considered the nycteolines to be a subfamily of the arctiids, closely related to the Nolinae and this postulated relationship was to recur later.

The three classifications

By 1900, there were three main arrangements of the noctuid genera in use, those of Grote, Hampson and Tutt.

Grote's classification was the only one not based upon the families of Guenée, groups that Grote still maintained had no value. The use of his classification was largely confined to North America.

Hampson's classification was a less well-resolved version of Guenée's. It was followed without alteration by Leech (1900) while Staudinger & Rebel (1901) modified it slightly. They reintroduced the Acronyctinae, with the usual constituent genera – *Panthea, Trichosea, Moma, Demas* [*Colocasia*], *Acronycta* [*Acronicta*], *Simyra,* etc. – but retained *Bryophila* [*Cryphia*] in the Trifinae. The latter subfamily was expanded to include the Acontiinae and Euteliinae of Hampson. With no European representative, the Palindiinae and Stictopterinae were not considered. The Sarrothripinae were united with the chloephorines (e.g. *Earias*) and placed in a separate family, the Cymbidae, between the Nolidae and the Syntomidae [Arctiidae: Ctenuchinae]. Thus, where the sarrothripines were concerned, Staudinger & Rebel chose to accept Dyar's conclusions. The Gonopteridae and Deltoidinae were retained while the Focillinae were included in the Quadrifinae.

Whereas the other two systems had undergone only minor alterations, Tutt (1902) introduced considerable changes into his classification of the Noctuidae (Table 8).

The Noctuides. Despite the opinions of Grote and Hampson, Tutt still clung to the earlier ideas regarding the evolution of the noctuids. The Deltoides were considered to be the most primitive group from which at least two independent lines had evolved. One of these lines proceeded through the Minores, Genuinae and Bombycoidae to the Arctiidae and Lyman-

Table 8 The classification of the Noctuidae followed by Tutt (1902). It represents a modified version of Guenée's second classification.

Family: 1 Bombycoidae
Family: 2 Noctuidae
- Subfamily: 1 Noctuinae
  - Tribe: 1 Leucaniidi
  - 2 Agrotidi
- Subfamily: 2 Caradrinae
  - Tribe: 1 Stilbidi
  - 2 Caradrinidi
- Subfamily: 3 Amphipyrinae
- Subfamily: 4 Apameinae
  - Tribe: 1 Nonagriidi
  - 2 Apameidi
  - 3 Carpocapsidi
  - 4 Bryophilidi
  - 5 Hadenidi
- Subfamily: 5 Orthosiinae
  - Tribe: 1 Orthosiidi
  - 2 Cosmiidi
- Subfamily: 6 Calocampinae
  - Tribe: 1 Xylocampidi
  - 2 Calocampidi
  - 3 Cuculliidi
- Subfamily: 7 Heliothinae
- Subfamily: 8 Plusiinae

Family: 3 Acontiidae
- Subfamily: 1 Acontiinae
- Subfamily: 2 Erastriinae
- Subfamily: 3 Anthophilinae

Family: 4 Catocalinae
- Subfamily: 1 Catocalinae

Family: 5 Aventiidae
Family: 6 Phalenidae
Family: 7 Euclididae
Family: 8 Poaphilidae

triidae, while the other passed through the Catocalinae to the geometrids. The Geometridae were therefore highly evolved noctuids.

Bombycoidae. Tutt considered that the larvae of this group resembled the Arctiidae and Liparidae [Lymantriidae] and that these families may therefore have evolved from bombycoid stock. Following Grote, rather than Hampson, Tutt accorded this group family status.

Noctuidae. This family was essentially the equivalent of Guenée's Genuinae but with the addition of the Bryophilini, Stilbidi, Amphipyrinae and Plusiinae. Eight subfamilies were recognised.

Noctuinae. Although Tutt divided the subfamily into three tribes (Leucaniidi, Agrotidi and Noctuidi), he treated the genera of the last two together as the Agrotidi. The Leucaniidi contained the hadenine wainscots and the Agrotidi coincided for the most part with the present Noctuinae.

Caradrininae. Two tribes of small inconspicuous moths formed this subfamily. The Stilbidi included *Stilbia, Hydrilla* [*Hydrillula*] and their relatives, while the Caradrinini included such genera as *Laphygma* [*Spodoptera*, part].

Amphipyrinae. This tribe contained only two species, *Amphipyra pyramidea* and *A. tragopogonis*, characterised by their ability to secrete themselves into narrow crevices.

Apaminae. Tutt considered this family to have been 'wonderfully muddled by British authors'. He recognised the superficial similarities between the Nonagriidi and the Leucaniidi (Noctuinae) as convergent. Five tribes were included.

The Nonagriidi consisted of those wainscots with stem-boring larvae.

The Apameidi were dull-coloured and had larvae that were either root-borers or fed on low plants, often on their roots (e.g. *Gortyna, Xylophasia* [*Apamea*] and *Miana* [*Oligia*]. Most are now amphipyrines but there are some hadenines and noctuines.).

The Carpocapsidi (*Dianthoecia* [*Hadena*]) were distinguished by the larvae feeding exclusively on the seed-capsules of the Caryophyllaceae.

Tutt removed *Bryophila* [*Cryphia*] from its usual place near *Acronicta* and placed it in a separate tribe in the Apameinae, the Bryophilidi. He considered *Bryophila* to be a hadenoid genus, related to *Hecatera* [*Hadena*].

The last tribe of this group, the Hadenidi, was one that had been merged with the Apameidi by other authors but which many British lepidopterists thought deserved family rank. Tutt concurred with the former, being unable to find any significant distinction between the two groups, but he nevertheless retained the Hadenidi as a separate entity. Included were amphipyrines, cuculliines, and hadenines.

Orthosiinae. The moths that comprised this subfamily were characterised by being on the wing either very late or very early in the year. Two tribes were recognised.

The Orthosidi was a mixed bag of genera, with representatives from the present Hadeninae (e.g. *Taeniocampa* [*Orthosia*]), Cuculliinae (e.g. *Xylina* [*Lithophane*]) and Ophiderinae (*Gonoptera* [*Scoliopteryx*]).

The second tribe, the Cosmidi, was distinguished from the last by the larval habit of spinning leaves together. All are now placed in the Amphipyrinae and include such genera as *Dicycla* and *Calymnia* [*Cosmia*].

Calocampinae. Tutt followed Grote (1895*b*) by separating *Xylina* [*Lithophane*] from the other genera previously placed in the 'Xylininae'. The remaining group was termed the Calocampinae and consisted of three tribes: the Xylocampidi (*Xylocampa*), the Calocampidi (*Calocampa* [*Xylena*] and *Lithomia* [*Lithomoia*]) and the Cuculliidi (*Cucullia*).

Heliothinae. The moths of this subfamily were characterised by the generally diurnally-active, colourful adults and flower-feeding larvae. All the British species currently assigned to the Heliothinae were included, together with the hadenine *Anarta* and the amphipyrine *Heliaca* [*Panemeria*].

Plusiinae. Tutt now considered this subfamily to be a highly-developed group of heliothines. The reduction in the number of larval prolegs (which also occurs in other groups of noctuids) was explained as the result of convergent evolution. Only the species currently placed in this subfamily were included. Its position in the Trifidae agreed with Grote's system rather than with Guenée's.

Acontiidae. This family was believed by Tutt to be closely related to the Deltoides, from which they might have arisen. Three subfamilies were recognised.

The Acontiinae contained *Agrophila* [*Emmelia*] and *Acontia* [*Tyta*]. *Erastria* [*Lithacodia, Elaphria*] and *Banksia* [*Eustrotia*] comprised the Erastriinae while the Anthophilinae contained *Hydrelia* [*Eustrotia*] and *Thalpochares* [*Eublemma*]. All except *Tyta* (Ophiderinae) and *Elaphria* (Amphipyrinae) are currently acontiines.

Geometriform noctuides. At this point in the family, Tutt's nomenclature and ranking broke down, mainly because the groups concerned were poorly represented in the British fauna. Nevertheless, he considered the British species could still give some indications as to the evolutionary history and development of the Geometridae. The families discussed below, together with the Trifidae, were considered to have all arisen independently from the deltoids.

Catocalidae. Only one subfamily, the Catocalinae, was represented in Britain. This was the group Tutt considered to be closest to the geometrids, a relationship he thought was more obvious in certain exotic groups than in the single British genus, *Catocala*.

Aventiidae. This family contained only *Aventia* [*Laspeyria*] *flexula* and was erected because Tutt was unable to determine the nearest relatives of the species. The larvae have only three pairs of prolegs ('like some geometers') and a lateral row of fleshy filaments above the prolegs as in *Catocala*. The adult is deltoid in its general facies.

Phalenidae. Tutt retained this name for the family in preference to Brephidae. He interpreted the group as either being at a point early in the geometrid line of evolution or an isolated lineage, having undergone considerable parallel evolution with the Geometridae.

Serpentides. This group consisted of two families. The Euclididae contained the single genus *Euclidia* [*Euclidia, Callistege*], with larvae that Tutt considered to be 'remarkably geometriform'. He did not comment on the second family, the Poaphilidae, with its single species, *Prothymia* [*Phytometra*] *viridaria*. The former family is now part of the Catocalinae, the latter part of the Ophiderinae.

Deltoides. Tutt interposed the Geometridae between this group and the Noctuidae. He considered the Deltoides as a group, but not the individual species, to be ancestral to the other noctuid families. Three deltoid families were recognised.

Toxocampidae. This was a group of moths (*Toxocampa* [*Lygephila*] and *Ophiodes* [*Minucia*]) which Tutt considered to be essentially deltoid, but that also had certain affinities with the noctuids. Tutt was probably the only lepidopterist to associate these genera with the deltoids. At present, the former genus is ophiderine, the latter catocaline.

Hypenidae. Five genera (*Madopa* [*Colobochyla*], *Hypena, Bomolocha, Hypenodes* and

Thylomiges [*Tholomiges*]) comprised this family. Of these, the last four are still hypenines, while the first is placed in the Ophiderinae.

Herminiidae. This family was divided into two subfamilies: the monobasic Rivulinae (*Rivula*, now an ophiderine) and the Herminiinae, a group of three genera (*Hermina* [*Zanclognatha, Paracolax*], *Zanclognatha* and *Pechipogon* [*Herminia*]), commonly referred to as the 'fan-foots'.

Miscellanea. The Nolidae were considered to be related to the lithosiine arctiids, whilst the Nycteolidae [?Chloephorinae, ?Sarrothripinae] were a 'very highly developed group which has evidently been evolved from the Plutellidae or the Tortrices'.

Demas [*Colocasia*] *coryli* was placed in the Lymantriidae, while *Diloba caeruleocephala* was classified in the notodontid subfamily, Dilobinae. Also placed in a subfamily of the Notodontidae (as the Asterocopinae) were the two species of *Asterocopus* [*Brachionycha*]. Although noctuids according to virtually all previous authors, Tutt found it difficult to consider them as true noctuids despite their being 'undoubtedly closely allied'.

The Cymatophoridae [Thyatiridae] were considered to be equally closely allied to the Notodontidae and the Noctuidae (cf. Fig. 1).

These then were the three main systems for classifying the noctuids in use at the beginning of the twentieth century. However, in the period since the publication of *The Fauna of British India*, Hampson had also reassessed the interrelationships of the noctuid genera. This culminated in the publication of a system that was to become almost universally accepted and, in the long term, put the higher systematics of the Noctuidae into virtual stasis.

Demas [*Colocasia*] *coryli* – noctuid or lymantriid?

Before proceeding with Hampson's second classification, I shall return to the early 1890s to consider, in more detail, the controversy that surrounded the position of *Demas* [*Colocasia*] *coryli*.

Chapman (1893*a*) suggested that *Demas* should be returned to the family Liparidae [Lymantriidae], basing his conclusions upon the eggs, larvae and pupae. He also associated *Panthea coenobita* and *Diphthera* [*Trichosea*] *ludifica* with *Demas*, a group that was eventually to form part of the subfamily Pantheinae (see below).

Tutt (1895) criticised Smith (1893) for retaining *Demas* in its 'obsolete position . . . among the Noctuae', preferring to place the genus in the Lymantriidae.

Dyar (1895*b*) disagreed, drawing support from the studies of Poulton (1887). An investigation of the larvae of several Liparidae [Lymantriidae] had demonstrated the presence of dorsal eversible glands on abdominal segments 7 and 8 (more rarely on 8 only) in all species examined except *Demas*. If these structures proved characteristic of the family, then *Demas* had to be excluded. Dyar (1895*a*) had also found chaetotactic differences between the Noctuidae and the Lymantriidae, and showed that *Demas* conformed to the noctuid type. In addition, he (1895*b*) considered the adult to be more similar to the Noctuidae than to any other family.

Tutt (1896) replied to this, basing his conclusions upon the work of Chapman (1893*a,b*), then shortly afterwards, retired from the debate, having felt he had made his point. It thus befell Dyar (1896) to continue to press for the inclusion of *Demas* in the Noctuidae, by a reanalysis of Chapman's findings.

The eggs of *Demas* are vertically ribbed as in other noctuids, rather than obscurely ribbed or smooth as in the Lymantriidae. Chapman used characters such as the length and density of the setae, the form of the tubercles, especially the anterior trapezoidal (D1 sensu Hinton, 1946), and the colour. Dyar dismissed the first and last of these as being too likely to be subject to convergence while he suggested Chapman had been mistaken regarding the tubercle. In fact, *Demas* shows the strong tubercle of the noctuids rather than the condition found in the lymantriids, in which it is reduced or lost.

Dyar disputed Chapman's interpretation of homology between the dorsal glands of lymantriid

larvae and the mid-dorsal depressions found in *Demas*. To Dyar, the general facies of the larva of *Demas* was, if anything, arctiid rather than lymantriid. Overall, he concluded that Chapman's study supported the inclusion of *Demas* in the Noctuidae and not the Lymantriidae.

Grote (1896) followed Dyar, retaining *Demas* (as well as several other genera now considered to be pantheines) within the group he called the Apatelidae. However, no good adult character was given to differentiate the group from the Noctuidae and the larval characters upon which the Apatelidae was based were insubstantial.

Smith & Dyar (1898), using the conclusions reached previously by the latter author, restricted the family to include only *Demas, Panthea, Charadra, Harrisimemna, Merolonche, Arsilonche* [*Simyra*], and *Acronycta* [*Acronicta*]. *Raphia* and *Feralia* were rejected on larval characters, *Momophana* and *Moma* on adult characters. Of these four, the first is now an ophiderine, the next two cuculliines and *Moma* an acronictine.

Two series were recognised by Smith & Dyar. The first, the Pantheini, contained only *Demas, Panthea* and *Charadra* and was distinguished primarily by a quadrifine hindwing venation. Other characteristic features included hairy eyes, pectinate male antennae and a similar facies and pattern. *Raphia* also possessed these features although the hairs on the eyes are microscopic and the male genitalia are distinct. *Raphia* could not be placed satisfactorily and was therefore omitted from the Apatelidae.

The second series, the Acronyctini, consisted of the residual apatelid genera. It was characterised by a trifine hindwing venation. As this is also found in several other subfamilies, only the distinct larvae allowed Smith & Dyar to maintain the Acronyctini as a separate entity. In contrast, the Pantheini was a very distinct group of moths as adults, resembling the Acronyctini only in the larval stage. Smith & Dyar concluded that there was no real basis for a continued association between the two groups, as far as the adults were concerned. The two tribes were nevertheless collected into the noctuid subfamily Pantheinae.

The position of *Demas* in the Noctuidae was consolidated by the works of Staudinger & Rebel (1901) and Hampson (1898–1913). Only Tutt (1902) continued to regard the genus as a lymantriid.

Development of the Hampsonian monolith

The precursor

During the latter part of the 1890s, Hampson had been reappraising the classification of the Noctuidae. The new system, which appeared in part in Hampson (1900), was given in full in Hampson (1902).

A close relationship was still postulated between the Arctiadae [Arctiidae], Agaristidae [Noctuidae: Agaristinae] and the Noctuidae, and additionally, the Syntomiidae [Arctiidae: Ctenuchinae]. All these families agreed in having forewing vein M_2 approximating the lower angle of the discal cell. This character was also found in the Pterothysanidae, Lymantriadae [Lymantriidae] and Hypsidae [Arctiidae: Aganainae] and defined what Hampson termed the 'Noctuid group of families'. This grouping largely agrees with the present superfamily Noctuoidea (if one accepts the Notodontoidea as separate). The only exception to this is the Pterothysanidae, which is now placed in the Geometroidea, although the sole species considered by Hampson, *Pterocerota virginea*, may possibly be a eupterotid (R. Carcasson, manuscript note).

Hampson (1902) did not detail the reasoning behind his new system. The characters used to separate the subfamilies were given in a key (Table 9) and were based upon those of Lederer and Grote, although employed in a novel fashion.

The Agrotinae [Noctuinae] also included some of the species currently referable to the Heliothinae (e.g. *Melicleptria* [*Heliothis*]). The other trifine subfamilies were the Mamestrinae [Hadeninae], Polianae [Cuculliinae] and Caradrininae [Acronictinae + Amphipyrinae].

The quadrifine subfamilies comprised the Eutelianae [Euteliinae], Stictopterinae, Sarrothripinae, Acontianae [Chloephorinae], Homopterinae [Catocalinae], Mominae [Pantheinae], Plusinae [Plusiinae], Noctuinae [Ophiderinae] (and the chloephorine, *Earias*), Erastianae

Table 9 Key to the subfamilies of the Noctuidae recognised by Hampson in his second classification of the family (modified from Hampson, 1902).

1	Maxillary palps absent	2
–	Maxillary palps present	**Hyblaeinae**
2	M_2 hindwing obsolescent, crossveins m_1–m_2 and m_2–m_3 subequal	3
–	M_2 hindwing well-developed	6
3	Mid- and hind-tibiae spined	**Agrotinae**
–	Mid- and hind-tibiae not spined	4
4	Eyes hairy	**Mamestrinae**
–	Eyes not hairy	5
5	Eyes with long, overhanging cilia	**Polianae**
–	Eyes not ciliated	**Caradrininae**
6	Hindwing M_2 approximated to M_3 at base	7
–	Hindwing M_2 parallel to M_3	**Hypeninae**
7	Female frenulum simple	8
–	Female frenulum multiple	9
8	Lateral abdominal hair pencils present near anus	**Eutelianae**
–	Hair pencils absent, forewing with tufts of raised scales in cell	**Stictopterinae**
9	Male retinaculum bar-shaped	10
–	Male retinaculum not bar-shaped	11
10	Forewing with tufts of raised scales in cell	**Sarrothripinae**
–	Forewing without tufts of raised scales in cell	**Acontianae**
11	Midtibiae spined	**Homopterinae**
–	Midtibiae not spined	12
12	Eyes hairy	**Mominae**
–	Eyes not hairy	13
13	Eyes with long, overhanging cilia	**Plusianae**
–	Eyes not ciliated	14
14	Hindwing M_2 strong, from close to lower angle of cell	**Noctuinae**
–	Hindwing M_2 rather weak, from well above lower angle of cell	**Erastrianae**

[Acontiinae] (and several amphipyrines, e.g. *Cnodifrontia* and *Callopistria*) and Hypeninae.

Hampson retained the name Noctua but applied it to the ophiderine *Noctua strix* [*Thysania agrippina*]. This was the first species listed by Linnaeus (1758) in the 'genus' *Noctua* and so was designated the type-species, following Hampson's personal rule (that is, the first listed species when the genus was described; McDunnough, 1916). Thus, the group then currently known as the Noctuinae was termed the Agrotinae.

Hampson's Catalogue

The basic system of subfamilies was unchanged in Hampson's major work, the monumental *Catalogue of the Lepidoptera Phalaenae in the British Museum* (1898–1913). (Subsequent references to the Hampsonian system, unless qualified, refer to that proposed in this work.) The scheme of the phylogeny of the Lepidoptera as a whole had undergone some rearrangement from that published in *Fauna of British India*. The relevant parts of this new phylogenetic tree are shown in Fig. 2.

The major difference between Figs 1 and 2 is that, in the latter, the Noctuidae and related families were considered as terminal on the main stem, rather than being intermediate stages of development culminating in the Geometroidea. The relationship between the Noctuidae and Geometridae, as espoused by Tutt (1902), was thus rejected. The subgroups of the noctuids are discussed in detail below.

Volume 2 – Arctiadae: Nolinae [Noctuidae: Nolinae]. The nolines were retained by Hampson as a subfamily of the Arctiadae [Arctiidae]. They were considered to have arisen from very early arctiid stock, close to the noctuids *Hypena* and *Sarrothripus* [*Nycteola*] (with which they share the character of tufts of scales in the forewing cell). The similarity between the cocoons of the

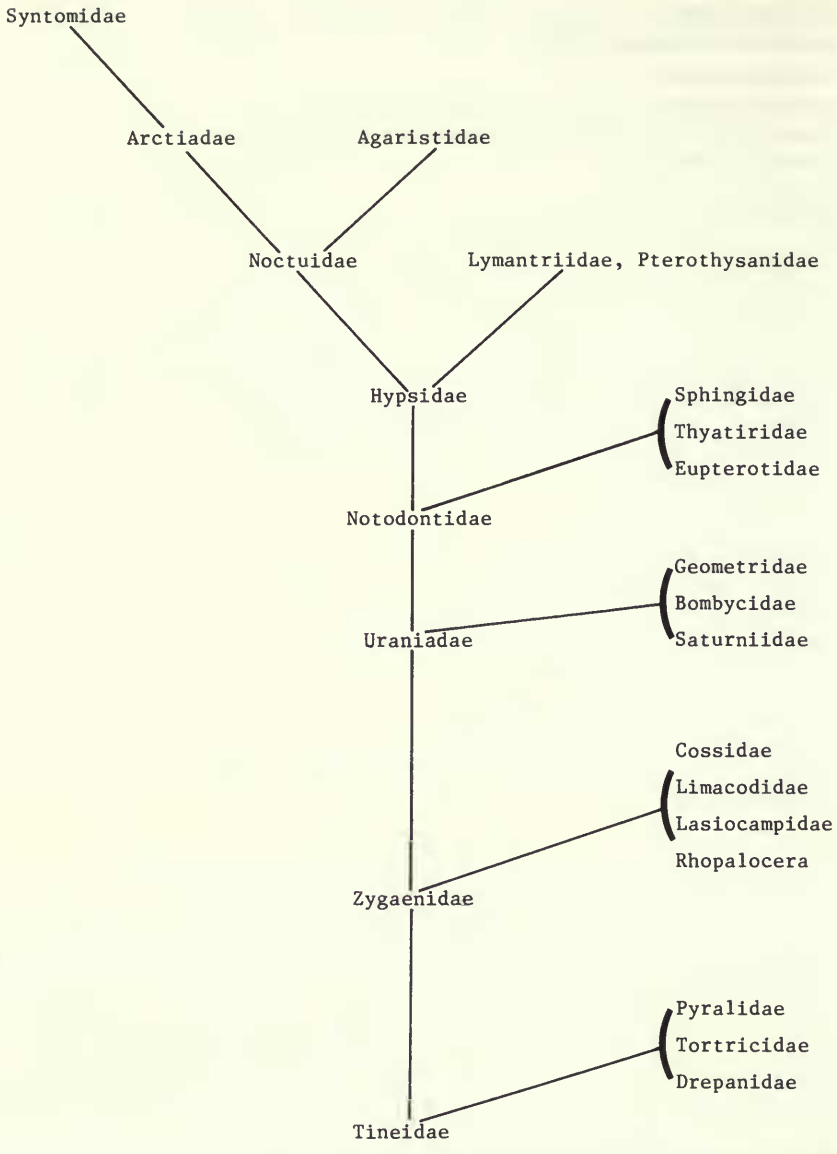

Fig. 2 Phylogeny of the higher Lepidoptera, with particular reference to the Noctuoidea, proposed by Hampson (1898–1913). There are several important differences from the previous phylogeny (Fig. 1). The noctuoid families are now considered to be terminal on the main stem and the arctiids are derived from the noctuids. In addition, the notodontids are now ancestral to the noctuids (the reverse relationship was postulated in Fig. 1). (Redrawn from Hampson, 1898–1913, **1**: 16.)

nolines and certain sarrothripines and chloephorines was also noted. Hampson excluded the latter two groups from the Arctiidae, considering them better placed in the Noctuidae because of the presence of ocelli and the free origin of hindwing vein $Sc + R_1$.

Volume 4 – Noctuidae: Agrotinae [Noctuinae]. This subfamily was characterised by a trifine hindwing venation and spined hind (and occasionally mid-) tibiae. Some species also had hairy or lashed (ciliated) eyes, characters of the Hadeninae and Cuculliinae respectively. This highlights a peculiar feature of the classificatory process as employed by Hampson. The major

(key) characters were treated as hierarchical. Thus, any trifine species with spined tibiae was placed in the Agrotinae irrespective of whether it also had the defining characteristics of the other subfamilies. Of the remaining species, any with hairy eyes were hadenines, though some also had lashed eyes. The cuculliines were those of the remainder with lashed eyes, while the residue, with none of these characters were, by default, acronyctines [Acronictinae + Amphipyrinae]. A similar but less hierarchical principle applied within the quadrifines.

This method of allocating genera to subfamilies can thus be seen to be arbitrary in those instances in which two or more characters conflict, due to the arbitrary order in which the key characters were ranked. Many of the species were misplaced (as considered by recent works) and it was from this realisation that the dissatisfaction with the system largely grew.

The Agrotinae contained two groups of genera corresponding to the present Noctuinae and Heliothinae (less the pyrrhine amphipyrines).

Volume 5 – Hadeninae. This group corresponded to the Mamestrinae of Hampson (1902). The included genera were hairy-eyed trifines with unspined tibiae, and a few (e.g. *Trichopolia* and *Stretchia*) also had lashed eyes.

Volume 6 – Cucullianae [Cuculliinae]. This trifine subfamily, previously referred to by Hampson (1902) as the Polianae, was characterised by bare, lashed eyes and unspined tibiae. In addition, many of the species appear as adults in the autumn or early spring, sometimes hibernating.

Volumes 7–9 – Acronyctinae [Acronictinae + Amphipyrinae]. This immense subfamily contained almost half of the then described genera of trifine noctuids. It was characterised by absences; no tibial spining and eyes devoid of hair and lashes. Hampson placed no special emphasis on the diverse hairy larvae of the acronictas, which were incorporated within the amorphous mass.

The Acronictinae were interpreted as the most primitive trifine subfamily from which the other three, together with the Agaristidae, had evolved as separate lineages.

Volume 10 – Erastrianae [Acontiinae]. This subfamily was the first of the Hampson quadrifine groups. Most genera had a strongly developed hindwing vein M_2, approximated at the base to M_3, but some had an almost typical trifine venation (e.g. *Eupseudomorpha, Cydosia, Graeperia* [*Heliodora*], *Tarachidia*). The last three of these remain acontiines but the first is now considered to be an agaristine. Overall, the subfamily was homogeneous in general facies but not well defined structurally. In many ways, it was intermediate between the trifine and the remaining quadrifine subfamilies. The larvae of most of the genera had the first one or two pairs of prolegs reduced or missing.

Volume 11 – Eutelianae [Euteliinae]. Characterised by a quadrifine wing venation, simple female frenulum and the presence of anal hair tufts in the males, this subfamily was essentially similar to that in Hampson (1893–5). He now considered this subfamily to be a parallel development, with the Stictopterinae, from the Noctuinae [Ophiderinae].

Volume 11 – Stictopterinae. This subfamily had also undergone little change. Its constituent genera also possessed the reduced female frenulum but had tufts of raised scales in the forewing cell and lacked the euteliine anal hair pencils.

Volume 11 – Sarrothripinae. This group was characterised by a bar-shaped retinaculum in the male and by tufts of raised scales in the forewing cell. An exception was *Eligma*, a genus now placed in the Chloephorinae (see below and also Mell, 1943). The larvae of the Sarrothripinae are sparsely covered in long hair and pupate in a boat-shaped cocoon.

Volume 11 – Acontianae [Chloephorinae]. Many genera of this subfamily also have a

bar-shaped retinaculum in the male. However, in *Earias*, *Tyana* and several other genera, this has been replaced by a tuft of hair. All are smooth-scaled except for *Cerala* [*Kerala*], which has slight scale tufts in the forewing cell. (Despite this, it was not placed in the Sarrothripinae, and still is not.)

The larvae of the Acontiinae, like those of the previous subfamily, have five pairs of prolegs and spin a boat-shaped cocoon on a twig, except for *Acontia* [*Xanthodes*], *Leocyma* and possibly *Armactica*, in which the larvae are semi-loopers and pupation takes place under- Hampson considered these genera might be better placed in the Erastrianae, which would then take the name Acontianae, whence the original Acontianae would become the Eariasinae.

Volumes 12–13 – Catocalinae. The Catocalinae was the first of two large sections into which Hampson divided the Quadrifinae of 1893–5. They were characterised by bare, unlashed eyes, normal frenulum and retinaculum, and spines on the mid-tibiae. Those Plusianae [Plusiinae] with spined tibiae could be distinguished by the presence of lashed eyes. However, Hampson did observe that many catocaline genera were closely allied to genera in the Noctuinae [Ophiderinae] and he considered it probable that either the Catocalinae were polyphyletic, with mid-tibial spines being multiply convergent, or that the Noctuinae were polyphyletic, characterised by multiple independent loss of spines. Either way, Hampson felt the two large subfamilies might have to be united as one large subfamily. Subdivision would then have to be on other grounds. Many of the larvae of the Catocalinae are semi-loopers, a feature Hampson considered to be convergent in this group and others such as the Plusianae [Plusiinae], Noctuinae [Ophiderinae] and Hypeninae.

Volume 13 – Mominae [Pantheinae]. This subfamily was equivalent to the tribe Pantheini of Smith & Dyar (1898). Hampson considered hindwing venation to be a more important character than larval facies and so removed the group from its association with *Acronicta* and its allies to a place among the quadrifine subfamilies.

Hampson considered the Mominae to be very natural and well characterised with two exceptions. Of these, *Elydnodes* is still a pantheine. However, *Epicausis* was transferred to the Cuculliinae by Viette (1962). On the basis of male and female genitalia, he placed it between *Daphoenura* and *Eudaphaenura*, genera that *Epicausis* also resembles in colour pattern. Viette also found that Hampson's interpretation of the hindwing venation was incorrect, for although M_2 is present, it is weaker than either M_1 or M_3. However, Viette neglected the fact that *Epicausis* has distinctly hairy eyes (which the other two do not; Kitching, pers. obs.) and thus resembles a third genus, the hadenine *Adaphaenura*, which also has a colour-pattern similar to that of *Epicausis*. Viette characterised the Hadeninae and Cuculliinae as having hairy and lashed eyes respectively, yet still placed *Epicausis* in the latter. With the involvement of mimicry a distinct possibility, the position of *Epicausis* and its putative allies must still be considered unsettled. Viette (1973) retained the genus in the Cuculliinae, as did Nye (1975).

Volume 13 – Phytometrinae [Plusiinae]. Using his personal rules for type-species designation mentioned earlier, Hampson considered it necessary to rename the group of moths that had been previously known generally as the Plusiinae. The subfamily consisted of those quadrifines with lashed eyes and included the monobasic genus *Diloba*, in addition to *Abrostola, Phytometra* [*Plusia* s.l., part] and their relatives. Apart from *Diloba*, which Hampson considered to be aberrant (for example, the larvae possessed five pairs of fully developed prolegs), the Phytometrinae were well circumscribed.

Diloba itself had been considered to be notodontid, acronictine or even thyatirid. Chapman (1893*a*) found the genus very difficult to place. The egg is macroscopically similar to *Acronicta*, but the sculpturing is different. The larvae of the two groups have little in common, while the pupal cremaster has a slight resemblance to *Bisulcia* [*Craniophora*] (Acronictinae). Overall, Chapman considered *Diloba* to be more bombycid than noctuid and suggested that it might require a family of its own.

Hampson, however, considered *Diloba* to be noctuid. Thus, because of a quadrifine hindwing venation and lashed eyes, it *had* to be placed in the Phytometrinae.

Volumes [14–16] (unpublished) – Noctuinae [Ophiderinae]. The publication of the *Catalogue* was suspended during the First World War for financial reasons. When Hampson retired in 1920, he left the manuscript covering the subfamily Noctuinae [Ophiderinae] (Gahan, Preface to Hampson, 1926). It is from that manuscript that the following is taken.

The Noctuinae were quadrifine noctuids with bare, unlashed eyes, which were distinguished from the Catocalinae by the unspined tibiae, and from the Polypogoninae [Hypeninae] by the third segment of the labial palp not being acuminate (most genera) and by hindwing vein M_2 being approximated to the lower angle of the cell. The labial palp segment three was always acuminate in the Polypogoninae while M_2 arises well above the lower angle of the cell and runs parallel to M_3 (except in the *Mastigophorus*-group).

The larvae all move in semi-looper fashion, even if all the prolegs are present (except for *Raphia*, whose affinities are open to question).

Hypeninae and Hyblaeinae. Hampson never dealt with these groups, the last two subfamilies of the Noctuidae as he conceived it (see Table 9).

The system proposed in Hampson's *Catalogue*, albeit unfinished, was to exert a profound influence on the higher classification of the Noctuidae and is still generally accepted today. But it is possible that it too might have gone down in history as just another arrangement, were it not for its acceptance and usage by the authors of Seitz' *Die Gross-Schmetterlinge der Erde*. This, more than anything else, was responsible for confirming the primacy of Hampson's classification in noctuid systematics.

Seitz' *Die Gross-Schmetterlinge der Erde*

The publication of the parts of this huge work that dealt with the Noctuidae spanned the years 1906 to 1944 and they were written by five authors – Jordan, Warren, Gaede, Draudt and Seitz himself.

Volume 3 – Fauna Palaearctica: Agaristidae (Jordan). Jordan (1906–14) followed Hampson in allying the Agaristidae [Noctuidae: Agaristinae] with the Noctuidae, considering them as merely 'day-flying Noctuidae which have preserved some generalised characters, being in other respects more spezialized [sic] than the Noctuids'. This interpretation was also espoused by Draudt (1919–44, Fauna Americana) and by Jordan & Gaede (1919–39, Fauna Africana). Originally the agaristines were placed at the head of the Bombyces, as a result of Linnaeus' (1758) opinion that antennal shape (i.e. clubbed) was of primary importance in the classification of the Noctuidae (Seitz, 1909).

Noctuidae (Warren). For convenience, Warren (1906–14) initially adhered to the five subfamilies used by Staudinger & Rebel (1901). The only change Warren introduced was to use the terms 'Trifidinae' and 'Quadrifidinae' for 'Trifinae' and 'Quadrifinae' respectively, because he considered the syllable 'fid' to be an integral part of the word upon which the name was based and not part of the family ending 'idae'.

With the publication of the first noctuid volume of Hampson's *Catalogue*, Warren chose to follow the new system as closely as possible but employing as few changes as possible also. As a result, complete correspondence with Hampson's subfamilies was not achieved (Table 10).

The Acronictinae, which also included the Pantheinae, was recognised as heterogeneous in wing venation but was accepted on the grounds that the included species had hairy larvae, which feed exposed, and that pupation takes place in a cocoon above ground.

The Metachrostinae, equivalent to the Bryophilidi of Tutt (1902), included only *Metachrostis* [*Cryphia*]. For the remaining noctuids, Warren thought it generally advisable to follow Hampson's arrangement.

Table 10 Sequence of noctuid subfamilies adopted by Warren (1906–14) in Seitz' *The Macrolepidoptera of the World*.

NOCTUIDAE
Acronictinae
Metachrostinae
Euxoinae
Hadeninae
Cucullianae
Amphipyrinae
Melicleptrinae
Heliothidinae
Erastrianae
Eutelianae
Stictopterinae
Sarrothripinae
Acontianae
Catocalinae
Phytometrinae
Noctuinae

The Agrotinae was renamed the Euxoinae, for unstated reasons. The Hadeninae and Cucullianae [Cuculliinae] were unaltered, while the Amphipyrinae represented the residue of Hampson's 'Acronyctinae' after removal of the Acronictinae (s.str.) and the Metachrostinae.

The Melicleptrinae, roughly equivalent to the present Heliothinae, was composed primarily of those trifine genera with curved fore-tibial claws.

The next subfamily, the Heliothidinae, has no modern equivalent. The genera that comprised it were characterised by small, reniform eyes (although Meyrick, 1912, regarded them as being more correctly termed ovate), a distinctly hairy vestiture and a primarily arctic-alpine distribution. Six unnamed divisions were recognised.

I. *Anartomorpha*. This genus combined the noctuine spined tibiae with the hadenine hairy eyes. Following Hampson's character hierarchy, it is currently placed in the Noctuinae (although it is treated as a hadenine, near *Anarta*, in the BMNH collection).

II. *Schoyenia, Orosagrotis* [*Euxoa* subgenus], *Grumia, Oxytypia*. Characterised by noctuine features, all these genera are currently placed in the Noctuinae (although *Grumia* is in the Heliothinae in the BMNH collection).

III. *Anarta, Panolis*. This division was characterised by hairy eyes and unspined, unclawed tibiae. Both genera are presently placed in the Hadeninae.

IV. *Omia, Sympistis, Hypsophila, Cteipolia*. These four lashed-eyed genera are currently placed in the Cuculliinae.

V. *Heliothis* [*Schinia*, part], *Pyrocleptria* [*Schinia*, part]. These two genera bear the spined tibiae of the Noctuinae and the clawed fore-tibiae of the Melicleptrinae [Heliothinae]. They are currently placed in the latter subfamily.

VI. *Xanthothrix, Apaustis, Panemeria, Janthinea, Stenoecia, Micriantha, Stemmaphora, Omorphina, Mesotrosta*. These genera comprised those with unadorned eyes and tibiae, and thus qualified as amphipyrines. All are currently accepted as such except *Omorphina*, which was classified by Hampson in the Plusiinae (Kostrowicki, 1961, considered it better placed in the Acontiinae).

Warren recognised the heterogeneous nature of this new subfamily, in that its members displayed all the features used to define the previous five groups. However, he considered the shared characters to be more important. The group was conceived to be the 'scattered remnants of archaic types, the conditions of whose existence synchronised with the more rigorous climate and scantier light of an earlier cosmic period'.

The Palaearctic genera of the Erastrianae [Acontiinae] were recognised to straddle the trifine-quadrifine border, in that they possess a strongly-developed hindwing vein M_2 (in contradiction to Hampson's key, Table 9) but the larvae, as far as were known, had a reduced number of prolegs. Warren treated them as intermediate between the other two large noctuid groups.

The remaining quadrifine subfamilies recognised by Warren coincided generally with those of Hampson. However, no distinction was made between the Noctuinae [Ophiderinae] and the Hypeninae, the combined group being referred to under the former name. *Diloba* was included with reservations within the Cymatophoridae [Thyatiridae] (Warren & Seitz, 1906–12).

Volume 7 – Fauna Americana: Noctuidae (Draudt). Draudt also largely adhered to Hampson's arrangement. However, the 'Acronyctinae' group [Acronictinae] was published before the volume in which Hampson merged it with the Amphipyrinae and so the division was maintained by Draudt. The Acronictinae was divided into two 'subordinate groups', the Mominae [Pantheinae] and the Acronictinae, which Draudt recognised as probably not being closely related but which were kept together in order to maintain the coherency of the entire work.

Warren's heliothidine genera were distributed among the other subfamilies (e.g. *Orosagrotis* [*Euxoa* subgenus] to the Agrotinae [Noctuinae] and *Anarta* to the Hadeninae). As a result, the group Warren termed the Melicleptrinae, which now contained *Heliothis* [*Schinia*, part], was renamed the Heliothinae and must have added greatly to the confusion of those using the work.

Unlike Warren, Draudt did separate the Noctuinae [Ophiderinae] and Hypeninae as distinct subfamilies (1919–44: 17) although only the ophiderine part was ever published.

Volume 11 – Fauna Indo–Australia: Agaristidae (Jordan). In this volume, Jordan (1912–14), in addition to his previous comments regarding this family, also added that it possibly ought to be merged with Hampson's Acronyctinae. Indeed, the latter author (Volume 9) included several agaristine genera in the Acronyctinae (e.g. *Xerocerus* to *Zalissa* inclusive). Jordan also thought it feasible that the Agaristidae were polyphyletic, with Old and New World forms representing distinct lineages.

Noctuidae (Warren, Gaede & Draudt). The trifine subfamilies were dealt with by Warren (1912–38), who retained the system he had used in the Palaearctic volume. The only alteration was the renaming of the Metachrostinae as the Bryophilinae. The majority of the quadrifine subfamilies, up to the Catocalinae, were described by Gaede (1937–38) and the remainder left to Draudt (1938). However, of the latter, only four lines of the introduction to the Phytometrinae [Plusiinae] were produced, the rest never being published. Both authors followed Hampson's arrangement of subfamilies.

Volume 15 – Fauna Africana: Noctuidae (Gaede). Several modifications were made to the arrangement employed in the previous volumes. Gaede (1913–39) followed Hampson in separating the acronictines and the momines [pantheines] into distinct subfamilies, although the two were still placed contiguously at the head of the family. In addition, the Sarrothripinae were divided into four informal groups:

(1) *Sarrothripus*-group: mostly very small with broad wings;
(2) *Eligma*-group: large and brightly coloured;
(3) *Gadirtha*-group: allied to the last in having long, subuliform palps and a dorso-ventrally flattened body, but being only half the size and cryptically coloured;
(4) *Blenina*-group: with cylindrical bodies and very broad, cryptically coloured wings.

Gaede also recognised the arbitrary nature of the division between the Catocalinae and Noctuinae [Ophiderinae] but considered that combining them, and perhaps also incorporating the Erastriinae [Acontiinae] and Hypeninae, would result in a very unwieldy group. Otherwise, Gaede saw no reason for separating such generic pairs as *Hypocala-Catocala, Fodina-Grammodes* and *Arcte-Cocytodes*.

This work, like many other volumes of Seitz, remained unfinished due to the destruction of the press and manuscript in the Second World War.

Satisfaction and apparent stability

The authors of 'Seitz' were not the only enthusiastic proponents of Hampson's subdivisions of the Noctuidae. Dyar (1904), in his review of the agrotine [noctuine] volume, considered Hampson's arrangement and use of characters 'highly commendable'. However, he was far from content with the nomenclatural changes imposed upon his native American fauna. In particular, Dyar objected to Hampson's refusal to adopt the names used by Hübner in the *Tentamen*.

Meyrick (1912), however, concurred with Hampson, reasoning that Hübner's names were invalid because they were published without accompanying descriptions. Meyrick did disagree with Hampson regarding the potential use of sexual characters to define genera, characters that were totally eschewed by the latter author. As a result, Meyrick found it difficult to accept many of Hampson's generic groupings. He did find some points of agreement with regard to the higher classification of the Noctuidae, which he was able to incorporate into his own arrangement of the New Zealand Caradrinina.

Meyrick employed the term 'Caradrinina' to cover the group today known as the Noctuoidea (s.str.), maintaining his view that the generic name *Noctua* and its associated group-names were inapplicable to this group of moths. In addition to the Arctiadae [Arctiidae] and the Hypsidae [Arctiidae: Aganainae], two other families were recognised. These were the Caradrinidae and the Plusiadae, direct equivalents of the Noctuidae and Plusiadae of his earlier (1887) work. In the present study, Meyrick chose to divide the families into subfamilies, largely following Hampson's usage. He did employ different names, however (Table 11). Of these, the Plusiades also included the ophiderines. Meyrick (1928) later employed the same scheme in his *British Lepidoptera*.

Table 11 The classification of the superfamily Caradrinina proposed by Meyrick (1912), the contents of which correspond to the current superfamily Noctuoidea, less the Lymantriidae and several small groups.

CARADRININA		
	Arctiadae	
	Hypsidae	
	Caradrinidae	
		Agrotides
		Poliades
		Melanchrides
		Caradrinides
	Plusiadae	
		Hypenides
		Catocalides
		Plusiades

Forbes (1914) implicitly adopted the Hampsonian subfamilies although he did not employ the names as such. He was also not impressed by the vagueness of the trifine-quadrifine border and referred to those in which the condition was doubtful as 'intermediid'.

Barnes & McDunnough (1917) were more faithful to Hampson's system. The only alteration was the substitution of Erebinae for Noctuinae [Ophiderinae].

Turner (1920: 120) went much further in his praise of Hampson: 'It would be difficult to over-estimate the debt which we owe to Sir George Hampson's great work. By it the study of the Noctuidae as a whole has been for the first time placed on a scientific basis'. Despite these words, Turner found it difficult, as did many other authors, to define the noctuid subfamilies precisely without recourse to 'distinctions of relatively trivial importance' (e.g. hairy eyes, spined tibiae, etc.). Overall, however, Turner considered it advisable to adopt Hampson's arrangement, primarily because no better system was available. This attitude was to become entrenched.

Turner formally relegated the agaristines to the rank of subfamily within the Noctuidae, and thus agreed with Mosher's (1916) findings on pupae (see below). He dismissed one of the usual defining characters (clubbed antennae) and could thus include several genera placed by Hampson in the Acronyctinae (as did Jordan, 1912–14). However, having done so, Turner was then quite unable to define the group.

The remaining subfamilies dealt with (up to the Acontianae [Chloephorinae]) remained unaltered, apart from the substitution of Hadeninae by Melanchrinae.

Hampson's arrangement was also accepted by Lhomme (1923–35) although again, the names of certain subfamilies had been changed (the Acronyctinae, Stictopterinae, Acontianae and Mominae became the Zenobiinae, Odontodinae, Westermanniinae and Diphtherinae respectively). This was in line with Hampson's supplement to the *Catalogue* (Hampson, 1918).

Similarly, minor nomenclatural changes apart, Hampson's subfamilies were adopted by Blackmore (1927). He agreed with Barnes & Benjamin (1923), in accepting that the Linnaean generic name *Phalaena* applied to the noctuids (rather than the geometrids, where it had more frequently been used). Hence, the family became the Phalaenidae and the subfamilies Agrotinae and Noctuinae [Ophiderinae] became the Phalaeninae and Erebinae respectively. (The family name Noctuidae was not finally stabilised until the suppression of *Phalaena* Linnaeus, 1758, by the International Commission for Zoological Nomenclature in 1957, Opinion 450.) Also, the Acronyctinae were referred to as the Apatelinae, presumably because Blackmore accepted Hübner's *Tentamen* and thus considered *Apatela* [*Apatele*] to have priority over *Acronycta* [*Acronicta*].

Finally, as an example of a study following Hampson almost to the letter, that of Prout (1929) might be mentioned. The only alteration employed was that she followed Comstock (1925) and regarded the hyblaeines as a family distinct from the noctuids (see also below).

Noctuoidea or Noctuidae?

A rather interesting variant of the Hampsonian system of families and subfamilies of the noctuoid group of moths was supported by some South African lepidopterists, notably Janse (1937–9). He considered the differences between the noctuoid families to be far too small compared to those found in other orders, and thus, following Handlirsch's (1929) suggestions regarding ranking, reduced them all to subfamilial level in a more inclusive Noctuidae (Table 12).

Inevitably, there were conflicts with Hampson's arrangement. The sarrothripines (as Nycteolini) were removed from the Noctuidae on the basis of a venational character (despite the 'shape of the forewings somewhat resembling those of the Acontinae' [Chloephorinae]) and placed as a tribe in the Arctiinae [Arctiidae]. Also the hypenines were recognised as a tribe of the Noctuinae, equivalent in rank to the trifines (Trifini) and the quadrifines (Quadrifini). Consequently, most of Hampson's subfamilies were relegated to the status of subtribes.

As to Hampson's subfamilial characters, Janse considered hairy eyes and tibial spines to be fairly reliable, at least with regard to excluding genera from his Acronyctae, while lashed eyes and the condition of hindwing vein M_2 were much less dependable. He also disapproved of the use Hampson made of thoracic and abdominal tufts and crests, preferring to delimit genera on the basis of structural characters, particularly those drawn from the male genitalia.

Only the Agaristinae and Noctuinae: Trifini: Acronyctae were covered by Janse (1937–9). The study was discontinued due to lack of material of non-South African type-species (Janse, 1942).

This arrangement of genera was also used by Van Son (1933), Janse (1939), and, in a modified form, by Kiriakoff (1963). The last of these works will be discussed in greater detail in a later chapter.

Hampson to the present day

Despite considerable reservations regarding the naturalness or, in practical terms, even the usefulness, of Hampson's subfamilial classification, most workers have continued to use it, for

Table 12 The concept of the Noctuidae employed by Janse (1937–9), which is almost identical to the current superfamily Noctuoidea. However, Janse did not consider the differences between the constituent groups (his subfamilies) to be great enough to warrant family rank.

NOCTUIDAE			
	Syntominae		
	Callimorphinae		
	Liparidinae		
	Arctiinae		
		Lithosiini	
		Nolini	
		Arctiini	
		Nycteolini	
	Agaristinae		
	Noctuinae		
		Trifini	
			Hadenae
			Agrotides
			Cuculliae
			Acronyctae
		Quadrifini	
			Momae
			Euteliae
			Stictopterae
			Acontiae
			Catocalae
			Plusiae
			Noctuae
			Erastriae
		Hypenini	

example, Zimmerman (1958), Common (1968), Pinhey (1975) and Leraut (1980). Several others have made only small modifications: Viette (1962–7) separated the Melicleptrinae [Heliothinae] from the Noctuinae; Boursin (1964) additionally accepted the Apatelinae [Acronictinae] (moves that were subsequently followed by Kloet & Hincks, 1972 and Bretherton *et al.*, 1979); while Forster & Wohlfart (1971) recognised the Apatelinae and the Bryophilinae but not the Heliothinae.

Thus it seems that, minor differences in opinion regarding the precise names of the subfamilies apart, Hampson's subdivision of the family could be regarded as definitive and dominant. However, although apparently stable and imperturbable, the system was challenged, even during its publication. Hampson's classification was based largely upon superficial characters of the adults and larvae. Detailed morphological and anatomical studies of all life-history stages were to cast serious doubt on the edifice. This doubt was eventually to lead to the proposal of a new system which, although still very much dependent upon that of Hampson, was to be more securely based in structural morphology.

The influence of immatures

Emergence

Most classifications of Lepidoptera have been derived using primarily adult characters. However, in several groups, of which the Noctuidae are one, the economic importance of the larvae resulted in studies from which grew the realisation that not only could larval characters be useful in identification but also in classification.

Forbes (1910) was one of the first to investigate thoroughly larval morphology. Several noctuid subfamilies were considered in detail and within the Noctuinae (sensu the Trifinae) in particular, Forbes discovered a highly uniform structure, despite much individual variation.

Only the tribes Acronyctini [Acronictinae] and Cuculliini [Cuculliinae] could be delimited using larval characters.

Fracker (1915) also investigated larval morphology but with special emphasis upon the chaetotaxy. He agreed with Hampson that the Nycteolidae ought to be reduced to a subfamily of the Noctuidae (Sarrothripinae), having found no significant chaetotactic differences between members of the two families. The larvae of the Agaristidae [Noctuidae: Agaristinae], apart from their bright transverse striping (also found in some other noctuids, e.g. *Acronicta alni*), were also indistinguishable from those of the Noctuidae and Fracker considered the family 'should meet the same fate as the Nycteolidae'.

Within the Noctuidae itself, Fracker found the same discouraging degree of uniformity. This prompted him to write: 'with the exception of half a dozen genera, noctuid larvae are so uniform that one can often compare, part for part, every segment and appendage of larvae of two species without finding a difference either of kind or of degree'. Fracker could only divide the family into four groups, three of which contained only members of the Acronictinae and Pantheinae, while the fourth comprised all the remaining subfamilies.

Mosher (1916) found a greater range of variation in pupae and was able to characterise tentatively 10 subfamilies (largely Hampsonian). One, the Agaristinae, was included perhaps for the first time as an explicit subfamily of the Noctuidae. As had been found for the larvae, no structural differences of the pupae could reliably distinguish the agaristines from the noctuids at the family level. The Acronyctinae were heterogeneous for, in addition to the acronictines *Eulonche* and *Acronycta* [both *Acronicta*] and the amphipyrine *Achatodes*, the division also included three ophiderines (*Homopyralis* [*Metalectra*], *Plusiodonta* and *Anomis*). However, Mosher did not consider that these genera formed a natural group.

Of the remaining subfamilies, members of the Catocalinae were distinguished by the presence of an alcohol-insoluble surface bloom, while the Sarrothripinae completely lacked a cremaster and spines (although Mosher did not consider this sufficient to warrant separation from the Noctuidae).

Ripley (1923) performed an extensive study of the morphology of larval noctuids but did not interpret the results taxonomically.

The larvae of the Hypeninae were examined by Crumb (1934), who discovered two distinct types. The first corresponded to Forbes' (1918) Herminiinae while the other was found not only in the remaining hypenines but also generally in the catocaline-erebine [ophiderine] complex. In this regard, the hypenoid type (as Crumb termed the latter form) was not particularly distinct from the majority of the Noctuidae. The herminioid type of larva was divided into two subgroups and the hypenoid type into five. On the basis of the larva, it was suggested that *Rivula* might merit a separate subfamily; it certainly was not hypenine.

Dethier (1941), in his detailed study of lepidopteran larval antennae, described those of the members of 10 noctuid subfamilies (including the Rivulinae). Apart from noting the great similarity between the Agaristidae and the Noctuidae, no further remarks were made regarding the higher classification.

The challenge from India

A major contribution to the understanding of the structure of larvae from outside the Holarctic was provided in a series of papers by Gardner on Indian Noctuidae. He subdivided the family, on the basis of previously defined larval characters (Gardner, 1941), into four groups, A–D, of which the first three were split further (Gardner, 1946*a*). The groups were not allocated formal names because of conflict with Hampson.

Division A (considered mostly in Gardner, 1946*b*) consisted of various trifine genera, the Agaristinae and some acontiines [chloephorines]. It comprised six sections.

A I: (described in Gardner, 1946*a*): Acronictinae, Pantheinae and *Cetola* (Amphipyrinae). The larva of the last genus was not distinctly hairy but was included because it had six setae on the external surface of the prolegs rather than three.

A II: Amphipyrinae, Hadeninae; also *Agrotis* [*Xestia*] *c-nigrum* (Noctuinae) and *Lyncestis amphix* (Ophiderinae).

A III: Noctuinae (*Agrotis* and *Euxoa*).

A IV: (described in Gardner, 1946*a*): Heliothinae (*Heliothis, Pyrrhia* and *Adisura*).

A V: Acontiinae [Chloephorinae] (*Aiteta, Carea, Maurilia, Pseudelydna*).

A VI: Amphipyrinae (*Callyna*), Hadeninae (*Tiracola*), Chloephorinae (*Churia*), Agaristinae (*Aegocera, Eusemia*).

Division B (mostly dealt with in Gardner, 1947) comprised those larvae in which the prolegs of abdominal segment 3 are abruptly reduced or absent. The distinction from the genera of division C, in which the prolegs are all equal or are only gradually reduced from segment 6 to 3, was considered to be somewhat arbitrary.

B I: (described in Gardner, 1946*a*): Acontiinae [Chloephorinae] (*Acontia* [*Xanthodes*]), Amphipyrinae (*Elydna, Chasmina, Androlymnia*), Erastriinae [Acontiinae] (*Amyna*) and Noctuinae [Ophiderinae] (*Bocula*).

B II: (described in Gardner, 1946*a*): Hypeninae (*Hypena, Dichromia, Rhynchina, Bomolocha*).

B III: Plusiinae.

B IV: Erastriinae [Acontiinae], Catocalinae (e.g. *Parallelia, Achaea*), Noctuinae [Ophiderinae] (e.g. *Othreis, Anomis*) and *Hypena* [*Sarobela*] *aurotincta* [*litterata*]. Group B IV was divided into three subgroups:
B IVa: lacking prolegs on abdominal segments 3 and 4;
B IVb: lacking prolegs on 3 only;
B IVc: prolegs present on 3 and 4, those of 3 distinctly reduced.

Division C (Gardner, 1948*a*), unlike A and B, was not subdivided. Instead, the genera were treated according to their Hampsonian subfamily. Included were the subfamilies Euteliinae, Sarrothripinae, Stictopterinae, Herminiinae, some Catocalinae and Ophiderinae, together with *Westermannia* (Chloephorinae) and the amphipyrines *Sesamia* and *Iambia*.

The final division, D (Gardner, 1947), differed from the others in setal group VI (part of the subventral group of Hinton, 1946) being bisetose on the meso- and metathorax rather than unisetose. Gardner considered that division D was artificial (he was eventually to conclude that the entire system was artificial; Gardner, 1948*a*), comprising as it did, *Brithys* (Hadeninae), *Selepa* (Sarrothripinae), and *Earias* and *Eligma* (Chloephorinae). These genera shared characters with the Lithosiidae [Arctiidae: Lithosiinae], Hypsidae (*Digama* [now an arctiine]) and the genera *Argina* and *Utetheisa* (Arctiidae: Arctiinae).

Gardner (1948*a*) considered that a natural classification of the noctuids should be based upon the number of setae in group VII (part of the subventral group of Hinton, 1946) on the first abdominal segment. This would divide the Noctuidae into two groups, representing roughly divisions A plus B, and C plus D, but with many exceptions.

The larval study was followed by a consideration of the pupae (Gardner, 1948*b*). The pupae of the Hadeninae, Amphipyrinae, Agrotinae [Noctuinae] and Heliothinae were all found to be very similar. Several genera (e.g. *Brithys*) that were distinct as larvae, proved equally distinct as pupae. The relationship between *Cetola* and the Acronictinae suggested by the larvae was not supported by the pupae. The Euteliinae proved to be very well defined by pupal characters. The genera of Acontiinae [Chloephorinae], which had been widely dispersed on the basis of larval characters, were all very close as pupae, except *Acontia* [*Xanthodes*]. They also shared features with the Sarrothripinae. No great distinction was found between the pupae of the Catocalinae and the Noctuinae [Ophiderinae], thus giving Mosher's surface bloom character wider significance.

Table 13 The division of the British Noctuidae proposed by Timlin (1955), based on larvae. NC = no comparison; [1] 1 = uniordinal, 2 = biordinal; [2] prolegs on abdominal segments 3 and 4 only partly developed; [3] except for certain *Cucullia* species.

Group	Proleg number	Secondary setae	Crotchets[1]	SV group of setae abdominal segment 1	Contents
1	5	+	1	NC	Most Acronyctinae [Acronictinae], *Dasycampa rubiginea* (Cuculliinae)
2	3	–	2	2	Plusiinae (*Plusia* [*Autographa*] *gamma*, *P.* [*Diachrysia*] *chrysitis*)
3	3	–	2	3	Plusiinae (*Polychrysia moneta*)
4	3	–	1	3	Ophiderinae (*Parascotia fuliginaria*)
5	4	–	1	3	Eustrotiinae [Acontiinae]
6	5[2]	–	1	3	Hypeninae
7	5	–	1	3	Plusiinae (*Episema* [*Diloba*] *caeruleocephala*), Ophiderinae (part), Acronyctinae [Acronictinae] (*Apatele* [*Acronicta*] *alni*)
8	5	–	1[3]	2	Agrotinae [Noctuinae], Hadeninae, Cuculliinae (except *D. rubiginea*) Amphipyrinae, Acronyctinae [Acronictinae] (*Cryphia perla* [*domestica*]), Sarrothripinae, Westermanniinae [Chloephorinae]

Further conflict

Timlin (1955) examined the larvae of 142 species of British noctuids, dividing the family into eight equivalent groups (Table 13). This arrangement was then contrasted with those of Hampson, Meyrick (1928) and Tams (unpublished). Tams' classification differed from Hampson's only in separating the Acronictinae from the Amphipyrinae.

Timlin found conflicts in the following areas:

(a) the heterogeneity of the Plusiinae, especially regarding *Episema* [*Diloba*];
(b) the similarity between the Hylophilidae [Chloephorinae + Sarrothripinae] and the Noctuidae;
(c) the reduction of the prolegs in the Eustrotiinae [Acontiinae];
(d) the lack of a distinction between the Catocalinae and the Ophiderinae;
(e) the high degree of similarity between the trifine subfamilies (less the Acronictinae).

In addition, Timlin considered the following genera might have been misplaced in classification based upon adult structures:

1, *Dasycampa* (Cuculliinae), which has secondary setae;
2, *Parascotia* (Ophiderinae), considered closer to the Hypeninae because of the reduced number of prolegs;
3, *Cucullia* (Cuculliinae), which is heterogeneous with respect to crotchet ordination;
4, *Scoliopteryx* (Ophiderinae), in which seta XD1 is nearer the midline than D1 on the prothorax, contrary to Fracker's (1915) diagnostic character for the Noctuidae;
5, *Episema* [*Diloba*], which, unlike the other plusiines, has five well-developed pairs of prolegs and uniordinal crotchets;

6, *Apatele* [*Acronicta*] *alni* and *Cryphia perla* [*domestica*] (Acronictinae), the only acronictines examined lacking secondary setae.

The next major work on noctuid larvae was that of Crumb (1956). He attempted to classify the larvae of as many North American genera and species as possible, in order to facilitate the identification of crop pests. The arrangement of subfamilies adopted is given in Table 14.

Crumb accepted the Agaristinae as a noctuid subfamily but did not discuss it further. He could not distinguish the Pantheinae and the Acronyctinae [Acronictinae] on structural grounds and so combined them under the latter name. The Heliothinae were found to be separable into two fairly good groups but Crumb did not apply the distinction.

Table 14 Arrangement of the noctuid subfamilies followed by Crumb (1956).

PHALAENIDAE
Agaristinae
Acronyctinae
Acontiinae
Cuculliinae
Euteliinae
Bagisarinae
Hypeninae
Phalaeninae
Hadeninae
Ufeiinae
Amphipyrinae
Plusiinae
Lithacodiinae
Sarrothripinae
Catocalinae
Herminiinae

Within the remaining subfamilies, apart from the unorthodox order of listing, several other innovations were proposed. New subfamilies were erected for *Bagisara* (Bagisarinae) and *Ufeus* (Ufeiinae). They are currently considered to be tribes of the Acontiinae and Noctuinae respectively (Franclemont & Todd, 1983). The Cuculliinae was restricted to the genera related closely to *Cucullia*, the others being placed in the Amphipyrinae. The Acontiinae was restricted to *Acontia, Tarachidia, Heliocontia* [*Spragueia*] and *Pseudalypia* (the Acontiini of Franclemont & Todd, 1983) while the remainder constituted the Lithacodiinae. The Amphipyrinae were divided into eight informal groups (three of cuculliines, three of amphipyrines and two mixtures). One of the mixed groups (number 6, *Pseudanarta, Proxenus, Anorthodes, Platyperigea, Xanthia, Sunira* and *Anathix*) was considered to be possibly natural.

The Catocalinae (including the Ophiderinae) was divided into six informal groups, which partially correlated with the groupings of Forbes (1954) (see also below) as follows:

1, Erebinae: Synedini;
2, Catocalinae: group 3; Erebinae: second miscellaneous series (part) (*Tathorhynchus*);
3, Catocalinae: groups 1 and 2 (parts); Erebinae: Erebini and Panopodini (part);
4, Catocalinae: groups 1, 2 and 4 (parts); Erebinae: Panopodini (part);
5, Erebinae: first miscellaneous series;
6, Erebinae: Anomiini and Scoliopterygini.

Beck (1960), in his study of the larvae of European noctuids, used a classification based upon Hampson but with several differences. The Noctuinae, Hadeninae and Zenobiinae [Amphipyrinae] were treated as tribes of the Noctuinae (following Börner's (1953) classification of the adults). The Cuculliinae and Heliothidinae [Heliothinae] were recognised as distinct trifine subfamilies. The Rivulinae and Herminiinae were recognised as separate while the remaining ophiderines were classified in the Catocalinae. Two tribes were recognised in the last subfamily,

the Catocalini (with two informal groups: *Laspeyria*/*Catocala*/*Mormonia*/*Minucia*; and *Euclidimera* [*Callistege*]/*Ectypa* [*Euclidia*]/*Lygephila*) and the monobasic Scoliopteryginae (*S. libatrix*). The ophiderine *Aedia funesta* was established in a separate subfamily, the Aediinae.

Merzheevskaya (1967) generally accepted an arrangement that was very similar to that of Beck (1960). However, the Agrotinae [Noctuinae] were divided into two tribes, the Triphaenini [Noctuini] and the Agrotini. One unusual move transferred *Amphipyra* to the Cuculliinae, resulting in the renaming of the Amphipyrinae as the Zenobiinae.

Godfrey (1972), following Hampson's definition of the subfamily, examined the larvae of many of the North American Hadeninae and divided the subfamily into 21 informal groups.

The most recent study of noctuid larvae (Arnold, 1982) was novel in that it looked not at the morphology of the larvae but at their haematocytes. Four basic types of cells were identified: plasmatocytes (of five varieties: standard, nematoform, lamellar, podoform and vesicular), granulocytes, spherulocytes and oenocytoids.

The species of Agaristinae, Pantheinae and Acronictinae examined all had only the basic cell types, in common with five arctiids, and this complement was interpreted as primitive. The Noctuinae fell into three natural groups, which showed little agreement with Forbes' (1954) divisions. The hadenines could also be divided into three groups on the basis of plasmatocyte type. The few cuculliines examined agreed with Forbes' subdivision; the three Cuculliini had only the basic complement while *Lithophane hemina* (Xylenini, Franclemont & Todd, 1983) differed in having lamellar plasmatocytes. The Amphipyrinae proved to be heterogeneous while the two heliothidines [heliothines] shared the unusual feature of the absence of spherulocyte staining.

Generally, classifications based upon noctuid larvae have proved to be at least partially incongruent with the Hampsonian system, while the degree of conformity with the newer arrangement exemplified by Franclemont & Todd (1983) remains to be seen. Larvae have proved to be potentially very useful in elucidating the higher classification of nymphalid butterflies (DeVries, Kitching & Vane-Wright, in prep.; Kitching, 1983, in press) where previous systems based upon adult characters have been shown to be incorrect by varying amounts. It seems likely, therefore, that no satisfactory arrangement of the noctuid genera into tribes and subfamilies can be achieved without reference to the immature stages and much work still remains to be carried out in this field.

The main assault

The gauntlet is thrown down

Tympanal organs: the development

Workers in noctuid systematics, from Guenée to Hampson, relied largely upon gross morphological structures to divide the group–wing venation, tibial spining, etc. The prime reason for the lack of study of other features, such as the arrangement of sutures and sclerites, was the presence of the characteristic scales of the Lepidoptera. Examination of surface structures would necessitate the removal of this vestiture, which was an anathema because of its effect on the appearance of cabinet specimens.

However, around 1910, attitudes began to change. The use of genitalia revolutionised lepidopteran systematics at the generic and specific levels, but the system that was to have the greatest impact on the higher levels was based on the tympanum.

It had been known for some time that such an organ existed (it was first referred to by Swinton, 1877) but it was Forbes (1916) who initially drew attention to the possibility of using it to help determine taxonomic relationships. Forbes (1918) employed the form of the tympanic hood to argue for the resurrection of the Herminiinae as a subfamily separate from the Hypeninae. Tympanal structures were also employed to argue that the anomalous arctiid, *Graphylesia*, was in fact a noctuid, related distantly to certain acontiine [chloephorine] genera (Forbes, 1924). The physiology and anatomy of the noctuid tympanum was further investigated by Eggers (1919; 1925).

Application

The wider systematic implications of the tympanum in the Noctuidae were left to Richards (1932). Drawing upon the studies of Shepard (1930), Richards made a highly detailed comparison of the morphology and evolution of the structure and divided the family as follows.

Herminiinae. Richards agreed with Forbes (1918) that this group was distinct from the remainder of the noctuids. The included genera all possessed a prespiracular tympanal hood (i.e. the first abdominal spiracle is posterior to and therefore outside the hood), as in the other noctuoid families (except the Nolidae and Agaristidae, see below), rather than a postspiracular hood (in which the spiracle is concealed beneath the hood). The former condition was considered to be primitive and led Richards to conclude that the Herminiinae were among the earliest offshoots from the noctuid lineage.

Rivulinae. Although the members of this rather ill-defined subfamily possessed the derived post-spiracular hood, Richards considered them to represent the most primitive noctuid subfamily. The remaining noctuid groups and the Herminiinae were interpreted as having been derived from the Rivulinae.

Rivula itself appeared to be the least specialised of all the Noctuidae examined by Richards, differing only slightly from the Hypsidae [Arctiidae: Aganainae] (although the latter has a *prespiracular* hood).

Hypeninae. Richards found it immensely difficult to subdivide the large group of genera comprising the Hypeninae, Catocalinae and Erebinae [Ophiderinae]. He was able to distinguish the genera near *Hypena* from the remainder of the Erebinae (except *Plusiodonta* and *Scoliopteryx*), considering them as a separate subfamily, the Hypeninae. (By way of an aside, Richards, in a footnote (10), stated that 'the immediate *Hypena* group and *Scoliopteryx* are the only quadrifids with lashed eyes outside the Plusiinae'. If this is true, then one can only conjecture as to why Hampson did not place at least the latter in the Plusiinae.) The Hypeninae were connected to the Rivulinae via *Pleonectyptera* [*Hemeroplanis*] and to more typical Erebinae via *Pangrapta-Herminodes*.

Three informal groups were recognised within the Hypeninae:

1, *Pleonectyptera* [*Hemeroplanis*], with an unspecialised tympanum;
2, the lashed-eyed hypenines, with a double pocket IV;
3, *Hormoschista* and its allies, with pocket IV yet further modified.

The erebine-catocaline complex. This group comprised Hampson's Catocalinae and Noctuinae. Richards, like Gaede (1913–39), considered the distinction based upon tibial spining to be completely artificial. However, unlike the latter author, Richards found he was able to divide the combined group, albeit based upon a limited sample of genera. Richards was very aware of the limitation this placed upon his conclusions.

The genera of the erebine-catocaline complex proved very diverse, falling into a number of relatively distinct groups which were connected by intermediate forms. Six such groups were recognised.

I. *Pangrapta/Gabara/Herminodes* group. This was the most primitive, from which the next group arose.

II. *Anomis/Calpe/Plusiodonta* group. This was considered to be rather artificial, connecting the previous series to the 'higher' erebines. *Alabama* and *Anomis* were considered to be extreme developments, while *Plusiodonta* was tentatively placed here, although it had more in common with the Hypeninae.

III. *Melipotis/Syneda* [*Drasteria*] group. Derived from the last mentioned, this was the most well-defined group of erebines, with a characteristic tympanal membrane and nodular sclerite. It includes *Leucanitis* and *Syneda* [*Drasteria*], genera currently assigned to the

Catocalinae and Ophiderinae respectively. These genera had tympana that Richards considered to afford 'good evidence of the artificiality of any division on spines'.

IV. *Euparthenos/Yrias* [*Metria*]/*Zale* group. Characterised by an overhung or pouched pocket I, this group was considered to have given rise to the Stictopterinae and Plusiinae (see below).

V. *Catocala/Erebus* [*Ascalapha*]/*Thysania* group. Richards considered this group to be rather artificially separated from the last.

VI. *Doryodes/Euclidia* group. This group, comprised of mainstream Catocalinae, was considered to be an independent derivative of group II.

Four genera were found to be very difficult to place: *Scoliopteryx, Gonodonta, Noropsis* [*Diphthera*] and *Litoprosopus*. The last of these was described as looking like 'a combination of a Notodontid and a Plusiid' and was highly anomalous.

Stictopterinae. Richards considered this subfamily to be derived from the Erebinae of group IV, and possibly to have given rise to the Plusiinae, 'for which they would serve as prototype'.

Plusiinae. This subfamily proved to be the most homogenous and distinct of the quadrifines. It was characterised by a double hood and a swollen area of the epimeron ventral to the tympanal membrane, which was the external manifestation of an enlarged pocket IV. (A similar bulge in other genera, notably the Herminiinae, is *ventral* to pocket IV.)

Euteliinae. This subfamily proved enigmatic. Generally, it was considered to be a development from the Erebinae, and would thus be placed near the Stictopterinae. However, the tympana of the euteliines have much in common with those of the Erastriini. Richards was undecided as to the position and affinities of the Euteliinae.

Erastriinae [Acontiinae]. Richards derived this subfamily from the lineage linking the Rivulinae and Hypeninae, and the Erebinae, via *Eublemma* [*Eumicremma* + *Eublemma*]. From this group could be derived the acontiine [chloephorine]-sarrothripine series and the trifine subfamilies. As mentioned above, the Euteliinae could be placed here also.

Two tribes were recognised by Richards. The Erastriini, in which the alula is unmodified, and the Tarachini, a very homogeneous group in which the alula is enlarged and strongly sclerotised. The tympanal membrane is concealed by the alula and the hood is correspondingly reduced or absent.

Acontiinae [Chloephorinae]. This subfamily combined the characters of both erastriine tribes and was considered to be derived from the last subfamily.

Sarrothripinae. Richards agreed with Hampson by placing this group as a derivative of the last, with which it shares many characters, especially internally.

Pantheinae. The relationships of this tympanally homogeneous subfamily were obscure to Richards. The form of the tympanum could be derived from that of the trifines, erastriines or even the erebines, and he was unable even tentatively to assign it a place on his phylogenetic tree.

The trifine subfamilies. These groups (Agrotinae [Noctuinae], Poliinae [Hadeninae], Cucculliinae and Acronyctinae [Acronictinae + Amphipyrinae]) were not examined in detail but appeared to be highly similar. Richards considered them to be developments from the higher erastriines with which they share many internal features.

Agaristidae. This family was considered to be derived from the Acronyctinae.

Nolidae. Richards concluded that this group did not belong in the Arctiidae, but was in fact very close to the Erastriinae, from which it could possibly be derived.

Richards synthesised his findings into a phylogenetic tree (Fig. 3). The arrangement, he concluded, was not substantially different from that of Hampson apart from the position of the Plusiinae, the unknown position of the Pantheinae and Euteliinae, and the division of the Catocalinae + Ophiderinae. However, it should be noted that there are several other major conflicts.

1. Hampson placed the Acontiinae [Chloephorinae] and Sarrothripinae between the Strictopterinae and the Catocalinae whereas Richards considered them to be derivatives of the Erastriinae [Acontiinae] near the trifines.
2. The Rivulinae, noctuines [ophiderines] according to Hampson, were given subfamilial status and considered to be the most primitive noctuids by Richards.
3. The Herminiinae were separated from the Hypeninae.
4. The nolids were associated with the 'higher' noctuids rather than with the arctiids.

Thus Richards' work provided evidence that cast serious doubt upon many of the Hampsonian subfamilial relationships. Nevertheless, it was based, for the most part, on a single organ system, the components of which are not readily observable. It was also based upon observations on only a very small percentage of the species of Noctuidae, whereas Hampson's arrangement was constructed after study of most of the then-known species. The influence that Richards' work was to have, and its potential was great, remained to be seen.

The cause is taken up

Initial acceptance in the U.S.A.

The main proponent of the taxonomic use of tympanal organs in noctuid classification continued to be W. T. M. Forbes. However, even he was disinclined to change the accepted classification (i.e. Hampson's) to conform with the more recent evidence (cf. Forbes' work on the phylogeny of the butterfly subfamily Danainae, reviewed by Ackery & Vane-Wright, 1984). Thus, in his study of the Lepidoptera of Barro Colorado Island (Forbes, 1939), he retained the nolids as a separate family (placed between the Euchromiidae: Ctenuchinae [Arctiidae: Ctenuchinae: Euchromiini] and the Arctiidae: Lithosiinae), despite noting that they possessed a tympanum similar to that of the Erastriinae [Acontiinae]. Similarly, the structure of the agaristid tympanum was mentioned as being 'of the Noctuid type' but the family status was retained and the group was left near the arctiids, between the Pericopidae [Arctiidae: Pericopinae] and the Lymantriidae.

McDunnough (1938) employed subfamily concepts (Table 15) based largely upon the work of Richards (1932) and the results of comparative studies of male genitalia, which were then being widely used following the pioneering work of Pierce (1909). The Pantheinae were associated with the Acronictinae at the head of the noctuids, a return to the older concepts of relationships rather than anything novel (but see below). The heliothines were separated from the agrotines (or phalaenines as McDunnough preferred to call them) and placed relatively distantly. The Catocalinae and Ophiderinae were considered to be one subfamily and the rivulines and herminiines were treated as distinct. The subfamily Hyblaeinae continued to be included in the noctuids, as the last listed. These three changes were revolutionary insofar as they were included in a major checklist for the first time and McDunnough's list was thus a step in the right direction.

The Lepidoptera of New York and neighboring states

The next stage in development was published by Forbes (1954). By including the results of the most recent studies on the Noctuidae, he was able to produce a classification that was the most detailed in its hierarchical structure since that of Tutt (1902) (Table 16). Based loosely upon Hampson, the noctuids were split into 14 subfamilies, many of which were further divided into tribes. In addition, and contrary to normal taxonomic practice, Forbes established 'miscel-

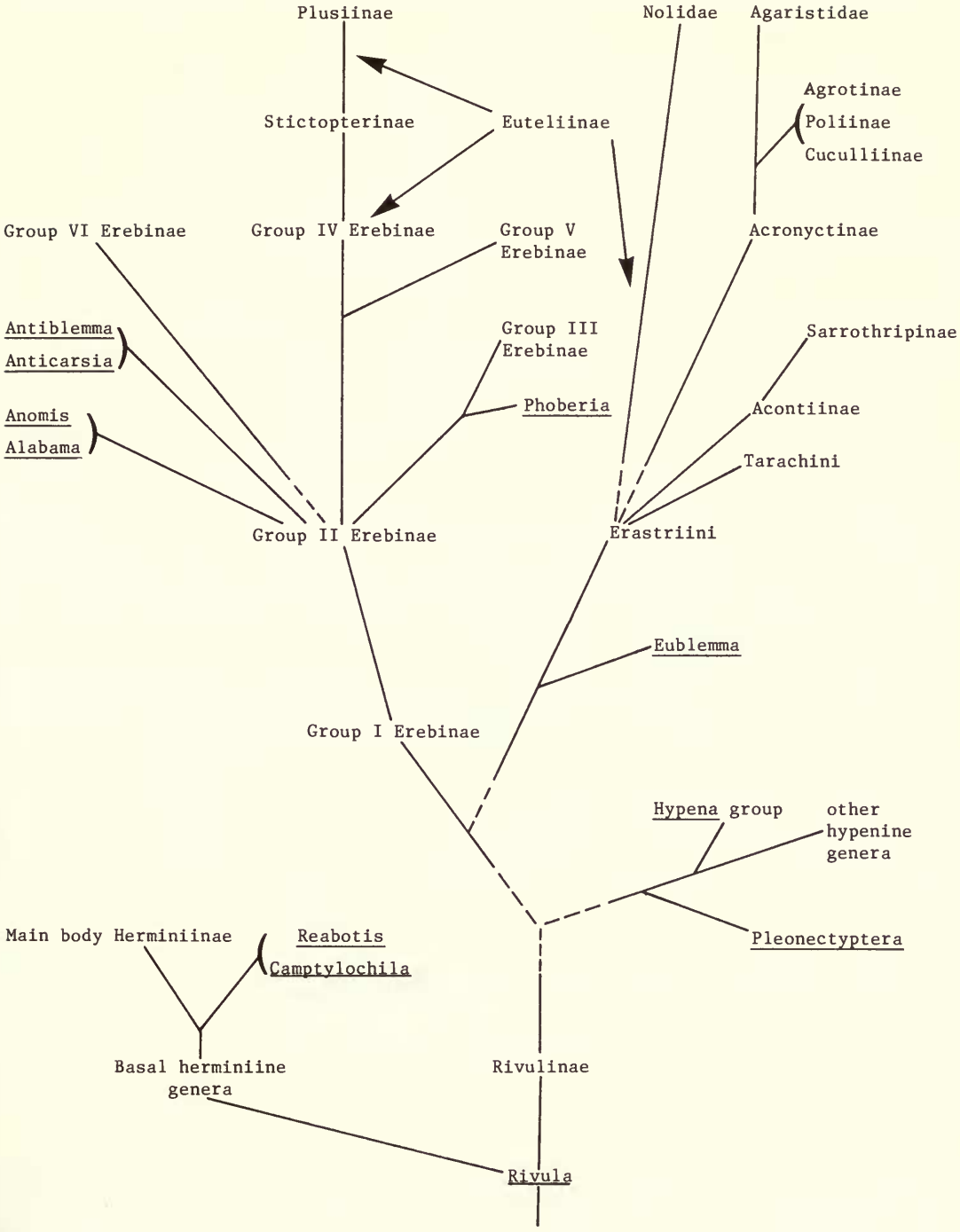

Fig. 3 Phylogenetic tree of the Noctuidae based upon characters of the tympanal organ (redrawn from Richards, 1932). Dashed lines indicate uncertain derivations, while the three arrows suggest three equally plausible positions for the subfamily Euteliinae: from the stictopterine-plusiine branch; from the group IV Erebinae; or from the Erastriini.

Table 15 Classification of the Phalaenidae [Noctuidae] employed by McDunnough (1938).

AGARISTIDAE	
PHALAENIDAE	
	Pantheinae
	Acronictinae
	Phalaeninae
	Hadeninae
	Cuculliinae
	Amphipyrinae
	Heliothinae
	Acontiinae
	Euteliinae
	Sarrothripinae
	Plusiinae
	Catocalinae
	Hypeninae
	Rivulinae
	Herminiinae
	Hyblaeinae

laneous series' and 'isolated genera', which were not assigned to formally named groups within subfamilies.

Agrotinae. Forbes used the family-group name 'Noctuidae' on the basis of '150 years of almost unchallenged use here and nowhere else'. However, he felt that to employ 'Noctuinae' for a subfamily would only invite confusion because of the previously diverse applications and so the term 'Agrotinae' was retained for the subfamily containing *Agrotis, Euxoa* and their allies. The Noctuinae of Hampson was termed the Erebinae.

Forbes divided the Agrotinae into two tribes. The first, the Heliothidini, was considered to be closely allied to *Agrotis*, although some authors (e.g. McDunnough, 1938) preferred to separate the two groups widely and derive the heliothines from the acronyctine tribe, the Pyrrhiini. The Agrotini was divided into three sections based largely upon genitalic characters. The main included genera in each were as follows:

group 1: *Agrotis, Eucoptocnemis, Copablepheron*;
group 2: *Peridroma, Pseudorthosia, Richia*;
group 3: *Noctua* [*Xestia*], *Eurois, Actebia, Cerastis*.

The first and last were considered to be fairly homogeneous, despite previous minute subdivision.

Hadeninae. Defined primarily on the presence of hairy eyes, Forbes considered this group to be fairly homogeneous although he had reservations regarding the amaryllidaceous-feeding genus *Xanthopastis*. Three subgroups were recognised on the basis of superficial characters:

1. a *Mamestra*-type, with rough, mixed vestiture and heavy tufting;
2. a '*Taeniocampa*'-type, with very smooth mixed vestiture, dull colouring and complete pattern; and
3. a *Leucania*-type, with fine, smooth vestiture, striate pattern and a grass-feeding larva.

However, the male genitalia did not agree with this division but instead suggested a large central homogeneous mass, from which individual genera and even species diverged. Also, many genera did not fit any of the above groups.

Cuculliinae. Forbes considered this subfamily to be possibly polyphyletic, with two series of tribes being independently derived from the Acronyctinae [Amphipyrinae + Acronictinae]. The first series (Cuculliini, Oncocnemidini and possibly the Psaphidini) were thought to be related to *Catabena, Oxycnemis* and some Stiriini, while the second series (Lithophanini,

Table 16 The classification of the Noctuidae proposed by Forbes (1954).

NOCTUIDAE
- Agrotinae
  - Heliothidini
  - Agrotini (divided into three informal groups)
- Hadeninae (divided into three informal groups)
- Cuculliinae
  - Cuculliini
  - Oncocnemidini
  - Psaphidini
  - Cleocerini
  - Lithophanini
  - Antitypini
- Acronyctinae
  - 'First series'
    - Septidini
    - Apameini (divided into two unnamed, intergrading subgroups)
    - Arzamini
    - Phlogophorini
    - Dipterygiini
    - Prodeniini
  - 'Second series'
    - Apatelini
    - Stiriini
    - Eudryini
    - Pyrrhiini
  - (the Acronyctinae also included many isolated and unplaced genera)
- Acontiinae
  - Eublemmini
  - Erastriini
  - Acontiini
  - (plus several other unplaced genera)
- Euteliinae
- Sarrothripinae
- Pantheinae
- Plusiinae
- Catocalinae (divided into four unnamed groups)
- Erebinae
  - Erebini
  - Panopodini
  - Synedini
  - Anomiini
  - 'First miscellaneous series'
  - Scoliopterygini
  - 'Second miscellaneous series'
  - 'Third miscellaneous series'
- Hypenodinae
- Hypeninae
- Herminiinae

Cleocerini and Antitypini) were conceivably related to such genera as *Andropolia, Rhizagrotis* and some of the Septidini/Apameini complex.

The Cuculliini comprised *Cucullia* only, and appeared to be closely related to the next, the Oncocnemidini, into which it intergraded in Europe. Containing six genera, the Psaphidini showed similarities to the last two tribes, as well as to the Lithophanini and the Antitypini. The Cleocerini contained only *Cleoceris* [*Brachylomia*] and *Litholomia*, while the Lithophanini, characterised by the presence of a well-developed digitus, was considered to be the dominant

group of cuculliines, with 17 included genera. Although the Antitypini formed a well-defined tribe in North America, Forbes was of the opinion that such was not the case in Europe.

Acronyctinae [Acronictinae + Amphipyrinae]. Despite its considerable size and degree of homogeneity, Forbes was able to subdivide this subfamily into two series of six and four tribes each. In addition, there were many unplaced, isolated genera.

First series. This group of tribes was polythetically defined by male genitalia with a normal corona, free pleurite with muscle-plate, lobed penicillus and a well-developed digitus. Six tribes were included: Septidini, Apameini (divided into two intergrading and unnamed groups), Arzamini, Phlogophorini, Dipterygiini and Prodeniini. In addition, eight isolated genera, which had some of the features of the Septidini, remained unplaced.

Second series. This group of tribes was characterised by the more or less general reduction or absence of a corona and digitus, an unlobed penicillus, no free ninth pleurite, a vinculum sometimes produced as a narrow strip, and larvae that are never borers or subterranean cutworms. Four tribes were recognised: Apatelini (equivalent to the most restrictive Acronictinae of previous authors), Stiriini (e.g. *Stiria, Plagiomimicus*), Eudryini (*Eudryas* and *Psychomorpha*) and Pyrrhiini (*Pyrrhia* and its allies). Three groups of isolated genera were also recognised:

(A) e.g. *Cosmia, Amphipyra*, with high-feeding, usually green, larvae;

(B) *Proxenus* and *Anorthodes*, with cryptically-coloured, brown larvae, feeding close to the ground or as a cutworm; and

(C) *Galgula*, with an unknown larva, about which Forbes would not conjecture.

Acontiinae. With regard to this subfamily, Forbes followed Richards (1932), but recognised three tribes, not two. The extra tribe, the Eublemmini, was erected to include *Eublemma* [*Eumicremma*] only which Richards considered to be a link with the deltoids. In addition, the Tarachini were renamed the Acontiini.

Euteliinae. Containing three genera (*Eutelia, Marathyssa* and *Paectes*), this subfamily was considered to be homogeneous and was unchanged from previous works.

Sarrothripinae. Considered to intergrade with the Nolidae in the Old World, the Sarrothripinae were believed to be 'an offshoot of the ancestral Noctuid type' (cf. Richards, 1932).

Pantheinae. This subfamily was considered to be generally well defined, although *Raphia* differed in its naked larva and in the hair on its eyes being microscopic.

Plusiinae. Despite being a distinctive subfamily, Forbes considered the Plusiinae might well be combined with the primarily Old World group, the Stictopterinae. In addition to the usual genera (*Abrostola* and *Plusia* s.l.), Forbes included *Phyprosopus*, because this aberrant genus would key out to this subfamily and a better position could not be suggested.

Catocalinae. Forbes recognised that the distinction between this subfamily and the Erebinae [Ophiderinae] broke down outside the Holarctic region but found it a useful concept within the North American fauna. On the basis of genitalic characters, the Catocalinae were divided into four relatively distinct groups, which were not formally named.

Erebinae. Forbes used Richards' analysis as a basis for his classification of this group. He agreed with Richards that all the other quadrifine subfamilies, bar possibly the Herminiinae, could be derived from it. Because the North American genera represented diverse elements and

any classification based upon these alone would be meaningless, Forbes chose to remove only five distinct groups as tribes and left the remainder in three 'miscellaneous series' corresponding to those groups to which they had been assigned by Richards.

Erebini. This tribe was characterised by such features as very short discal cells and distinctive tarsal spining and included *Erebus* [*Ascalapha*], *Thysania* and *Bendis* [*Lesmone*].

Panopodini. From the North American fauna, only *Panopoda* was included in this tribe. However, the group was much larger in the tropics, where Forbes suggested it might need subdivision. He also considered that the catocaline group 4 (*Zale* and *Euparthenos*) could be derived from a subgroup of the Panopodini.

Synedini. This tribe coincided with Richards' erebine-catocaline group III and, in Forbes opinion, was very homogeneous, with the exception of *Phoberia* and *Hypocala*.

Anomiini. This was another tribe Forbes considered to be well founded but for which he failed to elucidate the interrelationships within the subfamily. Consisting of *Anomis* and *Alabama*, the tribe corresponded to Richards' 'extreme development of group II'. Forbes also noted a possible affinity with the *Bagisara/Elydnodes* group of the Acronyctinae, and felt also that the genera *Amyna* and *Xanthodes* might belong in the Anomiini.

'First miscellaneous series'. This group represented those genera of Richards' group II that lacked the enlarged alula of the Anomiini.

Scoliopterygini. This erebine tribe (containing only *Scoliopteryx libatrix*) was characterised by strongly lashed eyes and a mixture of erebine and hypenine features.

'Second miscellaneous series'. The genera comprising this series were interpreted as the most primitive erebines by Richards but Forbes considered them to grade into the first miscellaneous series, via *Hypsoropha*.

'Third miscellaneous series'. Approximately equivalent to Richards' Rivulinae, this group was a mixture of primitive erebines.

Hypenodinae. This group was composed of the smallest of the noctuids and was characterised by the absence of ocelli (also missing in the sarrothripine *Comachara*). Forbes was uncertain whether the group deserved subfamilial or tribal rank.

Hypeninae. After removal of the Hypenodinae and the Herminiinae from the deltoids, the residue was placed in the Hypeninae, distinguished by long labial palps and lashed eyes.

Herminiinae. Forbes included 13 genera in this subfamily, which was characterised by a prespiracular tympanal hood.

The following were considered by Forbes (1960).

Agaristidae. The great similarity between this family and the Noctuidae (they were 'hardly distinct from the *Eudryas*-group of the Noctuidae'; but see below) did not influence Forbes and he maintained the two as separate entities.

Nolidae. This family was dealt with by Franclemont, who considered it to be derived from the sarrothripine noctuids and linked to them in the Old World by such genera as *Barasa*. Thus, any resemblance to the Lithosiinae (Arctiidae) was convergent. Nevertheless, the Nolidae were allocated their time-honoured position between the lithosiine arctiids and the Euchromiidae [Arctiidae: Ctenuchiinae: Euchromiini].

The system of Forbes was generally adopted by Inoue & Sugi (1958–61), although it differed in detail in several respects:

1, the Heliothidinae [Heliothinae], Apatelinae and Cryphiinae [both Acronictinae] were elevated to subfamily status;
2, Forbes' informal groupings of hadenines were recognised as distinct tribes: the Poliini, Orthosiini and Leucaniini;
3, no subdivisions were used in the Amphipyrinae, Acontiinae or Catocalini (which also included Forbes' Erebinae);
4, the Hypenodinae were not recognised.

In addition, the Sarrothripinae and Chloephorinae were merged as a single subfamily, the Nycteolinae.

This usage was important insofar as it represented the first occasion on which the new American classification had been applied to an Old World fauna.

Tympanal organs in Europe

While tympanal organs were having far-reaching consequences in noctuid taxonomy in North America, they were being virtually ignored on the other side of the Atlantic. Only Kiriakoff paid them any attention. In a series of 15 papers between 1948 and 1960, he studied many groups of the Noctuoidea, of which four are of direct relevance to the higher systematics of the Noctuidae.

The first (Kiriakoff, 1953) concerned the Hyblaeidae and will be considered further later.

The second (Kiriakoff, 1955) concluded that the Agaristidae were very close to the Noctuidae but separable on the basis of several structures, such as the pleural bulla (a large swelling at the base of the abdomen, visible externally).

Richards (1932) was uncertain whether the tympanal hood of the nolids was pre- or postspiracular, but Kiriakoff (1958) demonstrated the latter to be the case. He concurred with Richards and placed the nolids as part of the noctuid evolutionary line.

The final groups to be studied (Kiriakoff, 1960) were the herminiines, hypenines and rivulines. He agreed with Richards' distinction of the Herminiinae on the basis of the position of the tympanal hood but could not find any specific characters to allow either the separation of the Hypeninae from the Rivulinae or the differentiation of these two subfamilies from the erebine-catocaline complex. Characters such as the double pocket IV were considered to be unreliable because they 'occur in all the groups indiscriminantly'. As a result, and contrary to Richards, the Herminiinae rather than the Rivulinae were interpreted as the most primitive noctuids.

Kiriakoff (1963) eventually went even further. He proposed a classification of the Noctuoidea based upon the 'reduced rank' system of Janse (1937–9). *Endrosa* [*Setina*], a lithosiine with an unusual tympanum, was given family status in the Noctuoidea, equivalent in rank to a more inclusive Noctuidae. This family was divided into two subfamilies, the Arctiinae and the Noctuinae. The former, characterised by a prespiracular hood and a noctuid-type tympanum, also contained, in addition to the infra-families Arctiidi and Lymantriidi, the Herminiini. Within the Noctuinae, three infra-families were recognised: the Nolidi, the Noctuidi and the Agaristidi.

Kiriakoff considered his classification superior to older schemes 'because the tympanic structures undoubtedly are the most significant single set of characters that can be found in the Lepidoptera'. However, this confidence was not shared by other lepidopterists, who treated the single character complex-based classification with scepticism. It was never adopted as a serious alternative.

Recent developments in the U.S.A.

The latest higher classification of North American Noctuidae was presented by Franclemont & Todd (1983) (Table 17). Contrary to both Richards and Forbes, they consider the Herminiinae to be an advanced group of quadrifine noctuids, while the subfamilies closest to the ancestral stock of the Noctuidae are the Sarrothripinae and Acontiinae: Eustrotiini. Franclemont also recognises the very close similarity between the trifine subfamilies and would possibly advocate their amalgamation into a single subfamily, the Noctuinae. At most, perhaps two subfamilies

Table 17 The most recent classification of the Noctuidae, employed by Franclemont & Todd (1983). The 'Unassociated genera' of Amphipyrinae are those the authors did not assign to a particular tribe.

NOCTUIDAE
- Herminiinae
- Rivulinae
- Hypenodinae
- Hypeninae
- Catocalinae
- Plusiinae
  - Abrostolini
  - Plusiini
- Euteliinae
- Sarrothripinae
  - Risobini
  - Sarrothripini
  - Collomenini
- Nolinae
- Acontiinae
  - Cydosiini
  - Eustrotiini
  - Eublemmini
  - Acontiini
  - Bagisarini
- Pantheinae
- Acronictinae
  - Acronictini
  - Bryophilini
- Agaristinae
- Amphipyrinae
  - Apameini
  - Amphipyrini
  - Stiriini
  - Nocloini
  - 'Unassociated genera'
- Cuculliinae
  - Xylenini
  - Feraliini
  - Psaphidini
  - Oncocnemidini
  - Cuculliini
- Hadeninae
  - Hadenini
  - Eriopygini
  - Glottulini
- Noctuinae
  - Agrotini
  - Aniclini
  - Noctuini
  - Ufeini
- Heliothinae
  - [Heliothini]
  - Grotellini

could be recognised, the Noctuinae and the Acronictinae, the latter also including the pantheines.

Deltoids and Catocalinae. The deltoid subfamilies (Herminiinae, Hypeninae and Hypenodi-

nae) are largely unaltered, but there are many discrepancies with Forbes' classification regarding the remainder of the family. The Rivulinae represent the third miscellaneous series of Forbes' Erebinae, together with one genus from the second and three others. The remaining catocalines and ophiderines are combined into one large subfamily, the Catocalinae, which is not subdivided.

Plusiinae. The division of this subfamily follows Eichlin & Cunningham's (1978) revision although their Argyrogrammini and Autographini are merged to form one tribe, the Plusiini. *Phyprosopus* is transferred to the Catocalinae.

Euteliinae. This small subfamily is unaltered.

Sarrothripinae. Three tribes are recognised in this group. The Risobini comprises only *Baileya*; the Sarrothripini contains *Characoma, Nycteola* and *Iscadia*; while the Collomenini includes *Motya* and *Collomena* (two genera not considered by Forbes).

Nolinae. Franclemont & Todd include this erstwhile arctiid group in the Noctuidae and thus finally make one of the moves, which although mooted for decades, no-one had previously dared to perform.

Acontiinae. In addition to the three tribes (Eublemmini, Eustrotiini (Erastriini in Forbes, 1954) and Acontiini) previously employed, two more are also considered. The Cydosiini included only *Cydosia*, briefly discussed by Forbes under *Xanthoptera* [*Thioptera*], a genus of the Erastriini, while the Bagisarini included only *Bagisara*. This genus had been variously treated as an amphipyrine and an acontiine (the suggestion that it may belong in the latter subfamily was first made by Heinrich, 1926). Whereas Forbes treated *Bagisara* as an amphipyrine (although as an 'isolated genus'), Franclemont & Todd consider it to be an acontiine.

Pantheinae. This is the last quadrifine subfamily listed. The Pantheinae are removed from their Hampsonian position (before the Plusiinae, a placing followed by Forbes) and put next to the trifine subfamily Acronictinae. It would thus seem that the classification concerning the relative positions of these two groups has come full-circle.

Acronictinae. This subfamily is interpreted in the strict sense and is divided into two tribes, the Acronictini (*Acronicta, Simyra* and their allies, Forbes' Apatelini) and the Bryophilini, containing only *Cryphia*, a genus unconsidered by Forbes.

Agaristinae. Despite Mosher (1916) and Turner (1920), only lip-service had been paid to the high degree of similarity between this group and the Amphipyrinae. The inclusion of the agaristines as a subfamily of the Noctuidae was, like the Nolinae, the first occasion on which this had occurred in a major checklist. It is hoped that the false link with the Arctiidae and the unnecessary family rank have finally been laid to rest.

Amphipyrinae. The largest trifine subfamily is divided into four tribes followed by a large group of 'unassociated genera'. The Apameini is approximately equivalent to the tribes comprising Forbes' 'first series' combined, but also includes some of the 'isolated genera'. The classification of the Stiriini follows Hogue (1963) and corresponds to Forbes' Stiriini except for the removal of *Stiriodes* to the Amphipyrini. Seven genera constitute the Nocloini, none of which were treated by Forbes. The Eudryini are transferred to the Agaristinae (which Forbes considered they resembled) while the Pyrrhiini are incorporated into the Heliothinae. Of the remaining 55 genera, 30 form the Amphipyrini and 25 are 'unassociated'.

Cuculliinae. This subfamily is divided into five tribes. The Xylenini represents the combination of Forbes' Cleocerini, Lithophanini and Antitypini. *Feralia* is removed from the Psaphidini

to a tribe of its own (the Feraliini). This former tribe, and the Oncocnemidini and the Cuculliini, are largely unchanged.

Hadeninae. Unlike Forbes, Franclemont & Todd divide this group into three tribes: the Hadenini, the Eriopygini and the Glottulini. However, these groups do not correspond to Forbes' informal sections. The Eriopygini consists of a series of genera related to *Orthodes, Tricholita* and *Ulolonche*, while the Glottulini contains only *Xanthopastis*, a genus about which Forbes was unsure.

Noctuinae. The heliothines are excluded from this subfamily and the remaining genera are split among four tribes. The first three, the Agrotini, the Aniclini and the Noctuini, correspond to the first, second and third sections respectively into which Forbes divided the subfamily. The fourth tribe, the Ufeini, contains only the aberrant genus *Ufeus*.

Heliothinae. This subfamily comprises two tribes, most genera being included in the presumed Heliothini (the name is omitted). Following Hardwick (1970), Forbes' acronyctine tribe, the Pyrrhiini are also assigned here.

The second heliothine tribe, the Grotellini, contains only *Grotella, Hemigrotella* and *Neogrotella*, none of which was considered by Forbes. These genera were omitted from the Heliothidinae [Heliothinae] by Hardwick (1970), who suggested that they belonged in the Stiriinae [Stiriini] near *Stiriodes* (a genus Franclemont & Todd place in the Amphipyrini).

This then is the latest classification of the Noctuidae. It was produced from the results of many studies and is highly commendable. However, it must only be considered a starting point and it remains to be seen how well it will stand up in the face of future studies of noctuids from other parts of the world. What noctuid systematists outside North America cannot afford to do is to bury their heads in the Hampsonian sand and ignore this higher classification.

Novel character complexes

Scent brushes and hair pencils

The presence of various brushes, hair pencils and coremata, presumed to be associated with disseminating pheromones, have long been known in the Noctuidae (e.g. Pierce, 1909). Varley (1962) reviewed the structure and function of the brush organs of a number of noctuids and, unlike Pierce (1909), considered these organs to be potentially of great taxonomic value and urged further investigation.

Such a study was eventually carried out by Birch (1972*a*), who described the scent-brushes of a number of trifine groups. In a second paper, Birch (1972*b*) dealt with the relationship between chemistry and taxonomy.

The brush-organs were found to be composed of five separate structures. Birch considered there to be a particular order in which these components were lost and from this evidence concluded that the brush-organs of the trifine noctuids had arisen only once and that if a species lacked them, then it must be because of subsequent loss. The Acronyctinae [Acronictinae] were also found to lack these organs but in their case, Birch believed that this was due to their having split from the trifine lineage before the brush-organs first arose. On the basis of the most varied structure, the Cuculliinae were considered to have diverged next, followed closely by the Noctuinae. Most genera of the latter subfamily then lost their brushes. The apex of the phylogenetic tree was composed of the hadenines and the amphipyrines, which were impossible to subdivide. Hence, despite being extremely critical of the Hampsonian subfamilies, Birch, too, eventually had to use them in his final analysis. He therefore avoided the most controversial aspect of his work, that is, that the brush-organs could have suggested groupings of genera that were considerably at variance with those currently accepted.

Compound eyes

In an impressive study of the lepidopteran compound eye, Yagi & Koyama (1963) examined several noctuid species. Three groups of genera were recognised. Group 1 comprised catocalines and ophiderines only, while group 2 included five trifines, a plusiine and a hypenine. The species in these two groups are all nocturnal. The third group comprised the diurnally-active genus *Hyblaea*. On the basis of eye structure, Yagi & Koyama considered the hyblaeines (and also the agaristines) ought to be separated as distinct families (see also below).

This study, although superficial from the point of view of the Noctuidae, provided yet another means by which the higher classification of the Noctuidae might in future be tested.

A variation on the Sarrothripinae

Most workers in noctuid systematics recognise the great similarity between the Sarrothripinae and the Chloephorinae, in such features as the bar-shaped retinaculum (Hampson, volume 11), pupae (Gardner, 1948*b*) and tympanal organs (Richards, 1932). On several occasions, they had even been placed together in a separate family, the Hylophilidae (e.g. Staudinger & Rebel, 1901). Within the Hampsonian framework, the two groups were regarded as subfamilies of the Noctuidae, distinguished from each other on the basis of the presence or absence of tufts of raised scales in the forewing cell.

However, Mell (1943) considered the genera comprising the Sarrothripinae and the Westermanniinae [Chloephorinae] not to be sufficiently distinct to be worth regarding as separate subfamilies. Nor did he consider that they warranted even tribal status. Instead, Mell divided the more-inclusive Sarrothripinae into eight tribes and one species group, thus:

1, Eligmini – *Eligma, Selepa, Triorbis, Gadirtha, Lampothripa*;
2, Sarrothripini – *Sarrothripus* [*Nycteola*], *Bryophilopsis*;
3, Risobini – *Risoba*;
4, Blenini – *Blenina*;
5, Hylophilini – *Earias, Hylophilodes, Clethrophora, Hylophora* [*Pseudoips*], *Chloephora*;
6, Cymatophoropsiini – *Cymatophoropsis*;
7, Ariolicini – *Sinna, Gabala, Siglophora, Ariolica*;
8, Species-group *Tatothripa-Tympanistes*;
9, Careini – *Carea, Nertobriga*.

Of these, 2–4 contain only sarrothripines; 5, 7 and 9 only chloephorines; 1 is mainly sarrothripine with one chloephorine (*Eligma*); 8 also contains representatives of both (*Tympanistes* is the chloephorine); while 6 contains a genus currently assigned to the Ophiderinae. Unfortunately, no comparison is possible between the tribes of Mell and those of Francelement & Todd (1983) because there are no genera held in common except *Sarrothripus* [*Nycteola*].

This expanded concept of the Sarrothripinae was employed by Aubert & Boursin (1953), although the impoverished European fauna resulted in only two tribes being required, which, perhaps conveniently, corresponded to the previously accepted groups of the Sarrothripinae (as Sarrothripini) and the Chloephorinae (as Benini, = Hylophilini sensu Mell). Probably because the genera are mostly tropical, Mell's divisions have been largely ignored, and their usefulness, if any, must await a world-wide reappraisal of the group.

Mell (1943) also erected a new noctuid subfamily, the Camptolominae. This contained only *Camptoloma*, a genus that had until then been considered to be arctiid. Mell included it in the Noctuidae on the basis of forewing venation, and considered it close to the hylophiline sarrothripines because of similarities in the genitalia and immature stages. Inoue & Sugi (1958–61) considered the genus to be worthy of a separate family, while Nye (1975) and Inoue *et al.* (1982) place it in the Arctiinae. The systematic position of this genus remains in doubt but Inoue (pers. comm. to A. Watson) believes it to be more closely related to the Arctiidae than to the Noctuidae.

The removal of *Hyblaea*

The hyblaeines are small moths that superficially resemble stocky tortricids or miniature hypocalas (Noctuidae: Ophiderinae). On the basis of the latter resemblance, the group had long been considered to belong to the Noctuidae. Its position, as a subfamily of the Noctuidae, was virtually stabilised when it was accepted by Hampson. This was in spite of the well-developed maxillary palps, a feature unique in the Noctuidae.

The edict was first challenged by Comstock (1925) who considered the hyblaeines to be more closely related to the Thyrididae and placed the group accordingly after the pyraloids. The pupa was examined by Forbes (1933) and the supposed pyraloid affinities strengthened.

A thorough morphological study of the adult teak moth, *Hyblaea puera*, was performed by De Koning & Roepke (1949). They rejected the noctuid status of the species on the basis of:

1, absence of tympanum;
2, presence of three-segmented maxillary palps;
3, presence of an unusual secondary sexual organ on the male hind-tibia;
4, a tridentate uncus.

This last character agreed with the Thyatiridae (Pierce, 1909) but De Koning & Roepke could not include *Hyblaea* in this family because of venational differences. They also disagreed with Forbes (1933) contention that *Hyblaea* was pyraloid, although they were unable to suggest an alternative position.

Kiriakoff (1953) also noted a tympanum to be lacking in *Hyblaea* and therefore could not include the genus in either the Noctuoidea or in the Pyraloidea. Kiriakoff also reappraised the other structural characters of the Hyblaeidae. Although the family had much in common with the Tortricoidea, he eventually decided it represented a new superfamily, the Hyblaeoidea, related to the Notodontoidea and the Noctuoidea ('dans la sous-cohorte des Noctuiformes') but which had diverged from the main stem before the development of the thoracic tympanal organ in the latter groups. Later (Kiriakoff, 1963), he changed his mind, placing the Hyblaeidae in the Tortricoidea, and concluding that the family had nothing to do with the Noctuiformes after all. Despite this, most authors continued to regard the hyblaeids as either a family near the Noctuidae (e.g. Inoue & Sugi, 1958–61; Yagi & Koyama, 1963) or as a subfamily thereof (e.g. Viette, 1961).

Brock (1971) also excluded the hyblaeids from the Pyraloidea, including them in a new superfamily, the Aegerioidea, together with the Aegeriidae and the Dudgeoneidae. Pinhey (1975) noted the transfer but retained the hyblaeids at the head of the Pyraloidea.

Although Common (1975) criticised some of Brock's conclusions, the Hyblaeidae were not mentioned. However, Nye (1975) considered the Dudgeoneidae and the Hyblaeidae as pyraloid. Until the early stages are better known, the exact position of the Hyblaeidae remains doubtful.

***Diloba*: full circle – and back again?**

The early history of the aberrant species *Diloba caeruleocephala* was briefly discussed above. Several shifts in its systematic position had left it in the Plusiinae (Hampson, volume 13).

Richards (1932) examined the tympanum and found it to be typical of the Acronyctinae [Acronictinae + Amphipyrinae] and particularly similar to that of *Trachea*. Beck (1960) also included *Diloba* in the Apatelinae [Acronictinae] although the larva was aberrant in no less than six characters. However, most authors continued to consider it as either a pantheine (e.g. Aubert & Boursin, 1953; Heslop, 1960) or as a plusiine (South, 1961). Pierce & Beirne (1941) alone placed the species in the Lymantriidae, on the basis of the male and female genitalia.

Kiriakoff (1970) disagreed with Richards' (1932) conclusions, considering the tympanal organ of *Diloba* to be distinctly notodontid. However, *Diloba* differed from the Notodontidae in possessing 'a paired abdominal bulla operculated by the counter-tympanum, not unlike the structure found in the family Agaristidae' [Agaristinae]. Thus Kiriakoff found it necessary to place *Diloba* in the monobasic family, Dilobidae.

Tams (quoted in Varley, 1962, and pers. comm. to I. W. B. Nye, 1970) believed *Diloba* to be related to the cuculliine *Psaphida*. Minet (1982) reappraised the previous work on the tympanum and concluded that Richards (1932) had been correct in his interpretation and that Kiriakoff (1970) had been wrong. In addition, Minet (1982) suggested that *Diloba* fitted perfectly into the Cuculliinae (lashed eyes, obsolescent M_2 on the hindwing, cf. Hampson) and thus supported Tams' contention. Additional characters from the immature stages were used to support the inclusion of *Diloba* in the Noctuidae: eggs with radial ribs from the micropyle; larva with a prothoracic gland produced 'vertically' (as opposed to 'transversely' as in the Notodontidae) and having only a single pair of MD setae in the last larval instar (although this last character is plesiomorphic and therefore 'n'est pas significatif'). Minet did not apparently compare the genitalia of *Diloba* with those of cuculliines such as *Psaphida*.

Overall, however, the current consensus places *Diloba* either in the Notodontidae (a position followed by Kloet & Hincks, 1972; Bretherton *et al.*, 1979; Nye, 1975) or as a separate family (followed by Watson *et al.*, 1980; Leraut, 1980).

It would thus seem that, like the Hyblaeidae, the systematic position of *Diloba* is open to question yet. However, unlike the former, the problem of the affinities of *Diloba* is still firmly within the field of noctuid systematics.

The neglected arrangement

Preamble

By the 1920s, Hampson's system seemed to be the final word in noctuid higher classification. However, even before the dissatisfaction of workers such as Forbes set in, not all taxonomists were happy to accept the Hampsonian subfamilies. In particular, the amateur English lepidopterists rejected them, preferring to follow Meyrick, or even Guenée. After all, a new arrangement would have meant them re-ordering their collections. Eventually a classification arose that evolved into an arrangement of subfamilies which, although currently almost forgotten, bears much in common with the divisions of the Noctuidae employed recently by Franclemont & Todd (1983).

The demise of the systems of Guenée, Staudinger & Rebel and Tutt

The early part of the twentieth century saw the virtual disappearance of the noctuid classification of Guenée (1852–4) and those derived directly from it.

In his *Moths of the British Isles*, South (1908–9) followed the division of the Noctuidae employed by Staudinger & Rebel (1901). This survived until the revision by Edelsten & Fletcher (South, 1961), when the classification of Hampson was substituted.

Following the death of Tutt in 1911, a supplement to his *British Noctuae* was produced by Turner (1926–48). Although he discussed the classifications of the noctuids used by Hampson and in 'Seitz', in order to be consistent with Tutt's earlier work, Turner employed the arrangement used therein, namely that of Guenée. Thus Tutt's classification of 1902 fell into disuse. It was eventually followed by that of Guenée; Turner's usage was its last.

The English 'amateur' system

Origins

In 1907, Kirby published his *Butterflies and Moths of Europe*. In this, he acknowledged the classification of Staudinger & Rebel (1901) but preferred to use one of his own. This divided the Lepidoptera into 'macros' and 'micros'. The former was then further split into five 'superfamilies': Rhopalocera, Sphinges, Bombyces, Noctuae and Geometrae. Although Kirby removed the Cymatophoridae [Thyatiridae] from the Noctuae to the Bombyces (this heterogeneous group also contained the Nycteolidae [Sarrothripinae] and Chloephoridae [Chloephorinae]), the Noctuae still included the Brephidae [Geometridae: Archiearinae]. The remaining noctuids

were distributed among 18 subfamilies (Table 18), which appeared to have something in common with those of Herrich-Schäffer (1845) and part with those proposed by Grote in the 1880s and 1890s (see Tables 5 and 7), but also included some apparent influence from Hampson.

The Bombycoidae, a name which in various forms had previously been used to refer to several groups, here contained *Diloba* and the pantheines. These were followed by the Acronyctidae [Acronictinae] which, although it included *Bryophila* [*Cryphia*], omitted *Arsilonche* [*Simyra*] and *Simyra*. These last two genera were placed at the head of the subsequent group, the Orthosidae. This subfamily, which had previously been regarded as five (Leucaniidae, Caradrinidae, Orthosiidae, Cerastidae, Amphipyridae; Herrich-Schäffer, 1845), consisted mainly of hadenines, cuculliines (e.g. *Agrochola*) and amphipyrines, with minor representation from the Acronictinae (e.g. *Simyra*) and Ophiderinae (*Scoliopteryx*).

The Agrotidae, comprising mainly *Agrotis* (s.l.) and *Triphaena* [*Noctua*], was broadly equivalent to the Noctuinae, although it did include *Brithys*, a hadenine. The Hadeninae contained the balance of the hadenines and amphipyrines.

There followed several small subfamilies. The Xylinidae (e.g. *Xylina* [*Lithophane*], *Calocampa* [*Xylena*]), Cleophanidae (e.g. *Calophasia, Cleophana* [*Calophasia*, part]) and Cuculliidae (*Cucullia* only) contained most of the present Cuculliinae, although the first also included *Xylomiges* [*Egira*] (Hadeninae).

The Euteliidae (cf. Eurhipiidae in the introduction to Kirby, 1907, and Table 18) and the Heliothidae corresponded to the present subfamilies of the same names (the latter included *Pyrrhia* and its relatives). The next subfamily, the Anartidae, conformed to the residue of Warren's (1906–14) Heliothidinae after the removal of the true heliothines and it may be that Warren took over the concept from Kirby and expanded it. The Anartidae included representatives of the Amphipyrinae (*Euterpia* [*Enterpia*], *Heliaca* [*Panemeria*]), Noctuinae (*Cyrebia*), Hadeninae (*Anarta*) and Cuculliinae (*Omia*).

The Plusiidae included *Telesilla* [*Eucarta*], as well as the usual genera, *Abrostola* and *Plusia* (s.l.), while the Calpidae contained only *Calpe* [*Calyptra*]. The Acontiidae, including *Acontia* [*Tyta*], *Armada* [*Tarachepia*] and *Acontiola* [*Eustrotia* and *Ozarba*], was a mixture of ophiderines and acontiines. Most of the remaining catocalines and ophiderines were divided between the Catocalidae (e.g. *Catocala, Zethes, Aedia*) and the Ophiusidae (e.g. *Apopestes, Ophiusa* [*Lygephila*]). These two groups also contradicted those that Kirby, in his introduction (Table 18), said he was going to use (Ophiusidae and Toxocampidae).

Table 18 The subdivisions of the Noctuae [Noctuidae] employed by Kirby (1907).

NOCTUAE
Bombycoidae
Acronyctidae
Orthosidae
Agrotidae
Hadenidae
Xylinidae
Cleophanidae
Cuculliidae
Eurhipiidae
Heliothidae
Anartidae
Plusiidae
Calpidae
Acontiidae
Ophiusidae
Taxocampidae
Noctuophalaenidae
Deltoidae
Brephidae

The Noctuophalaenidae included the rest of the acontiines and the ophiderine, *Rivula*. The Noctuae finished with the Deltoidae (including the ophiderines *Laspeyria* and *Parascotia*) and the Brephidae.

Development

The arrangement of Kirby (1907) formed the basis of the system adopted by Heslop (1945) in his checklist of British Lepidoptera. It should be noted that Heslop, like many other earlier authors of checklists and catalogues, employed no new research, relying entirely upon the studies of others. His arrangement of the various groups was probably governed as much by personal taste as it was by explicit characters. Whatever his reasons, Heslop, again like many of his predecessors and several workers subsequently, never published his argumentation, thus rendering it virtually immune from objective criticism.

The noctuids were classed in the superfamily Agrotides and, following Meyrick (1928), divided into two families, the Caradrinidae and the Plusiidae.

Ten subfamilies were recognised in the Caradrinidae. Eight corresponded to those of Kirby: Mominae (Kirby's Bombycoidae), Acronictinae (Acronyctidae), Hadeninae, Caradrininae (Orthosiidae), Xyleninae (Xylinidae and also including the Cleophanidae), Cuculliinae, Anartinae and Heliothinae. The Agrotidae was split into two groups, the Agrotinae and the Triphaeninae. The Euteliinae have no British representatives.

The Plusiidae contained five subfamilies. The Catocalidae and Ophiusidae were combined under the Catocalinae, while the Acontiidae and Noctuophalaenidae merged to become the Eustrotiinae [Acontiinae]. The Deltoidae became the Hypeninae while the Plusiinae remained unaltered. *Scoliopteryx* was removed from the Orthosiidae and placed in a separate quadrifine subfamily, the Gonopterinae. The Brephidae, although listed after the Hypeninae, had been moved across to head the Geometridae as a subfamily of the Monoctenidae. In common with Kirby, Heslop placed the Westermanniinae [Chloephorinae] and Sarrothripinae, as subfamilies of the Hylophilidae, in the Bombyces.

Several changes were evident in the classification employed by Heslop (1960) in his revised checklist. Some subfamilies had been renamed as a result of considerable reassessment of the application of generic names that had been performed in the interim.

The superfamily was now known as the Noctuoidea, and the Caradrinidae as the Noctuidae. Similarly, the Triphaeninae had become the Noctuinae. The Hadeninae and Caradrininae had undergone extensive reassortment and had been divided into no less than seven subfamilies:

1, Hadeninae – those currently recognised hadenines, less the next two groups;
2, Orthosiinae – *Orthosia* and *Panolis*;
3, Leucaniinae – the hadenine wainscots;
4, Nonagriinae – the amphipyrine wainscots and *Stilbia*;
5, Caradrininae – *Caradrina* and its close relatives, *Meristis* and *Laphygma* [*Spodoptera*, part];
6, Apameinae – *Apamea, Luperina* and their allies, including also *Prodenia* [*Spodoptera*, part];
7, Amphipyrinae – the remaining amphipyrines, e.g. *Hydraecia, Cosmia, Mormo*.

Two series, 1–3 and 4–7, can be recognised as equivalent to the present Hadeninae and Amphipyrinae respectively.

The Acronictinae became the Apatelinae and finally, the cuculliine section of Kirby's Caradrinidae (e.g. *Antitype, Agrochola, Cirrhia*) was removed and established as the Dasypoliinae.

The second family of noctuoids was the Hylophilidae, finally recognised by Heslop as correctly belonging with the noctuids, and the third was the Plusiidae. The subfamilies of the latter group now largely agreed with those of Hampson, except that the Gonopterinae was retained. Consequently, the Pantheinae was moved into the Plusiidae from the Caradrinidae, and *Parascotia* and *Laspeyria* were transferred from the Hypeninae to the Ophiderinae.

Apart from combining the Xyleninae and the Dasypoliinae under the former name, the arrangement of Heslop (1960) was faithfully followed by Chalmers-Hunt (1962–8).

Was Heslop on the right track?

The most fascinating aspect to Heslop's (1960) classification of the Noctuidae is the degree to which it parallels that recently employed by Franclemont & Todd (1983). The two are compared in Table 19, demonstrating the considerable concordance, especially in the trifine subfamilies. There are, however, several discrepancies, which ought to be discussed further.

The British deltoid fauna is impoverished relative to that in North America (13 species, excluding *Laspeyria*, as opposed to 82) and so it is not perhaps surprising that Heslop did not consider it necessary to divide the Hypeninae, particularly as the study of the tympanal organ had not been influential in British noctuid systematics.

Table 19 A comparison of the higher classifications of the Noctuidae proposed by Heslop (1960) and Franclemont & Todd (1983).

Heslop	*Franclemont & Todd*
PLUSIIDAE	NOCTUIDAE
Hypeninae	Herminiinae, Hypenodinae, Hypeninae
Ophiderinae	Rivulinae, Catocalinae (part)
Catocalinae	Catocalinae (part)
Plusiinae	Plusiinae
Eustrotiinae	Acontiinae
Pantheinae	Pantheinae
—	Euteliinae
[Nolidae (Bombycoidea)]	Nolinae
HYLOPHILIDAE	
Sarrothripinae	Sarrothripinae
Westermanniinae	—
NOCTUIDAE	
Apatelinae	Acronictinae
—	Agaristinae
Cuculliinae	Cuculliinae: Cuculliini
Xylenini, Dasypoliinae	Cuculliinae: Xylenini
Amphipyrinae, Caradrininae	Amphipyrinae: Amphipyrini
Apameinae, Nonagriinae	Amphipyrinae: Apameini
Leucaniinae, Orthosiinae, Hadeninae, Anartinae	Hadeninae: Hadenini
Heliothinae	Heliothinae: Heliothini
Noctuinae	—
Agrotinae	Noctuinae

Heslop also retained Hampson's division into Catocalinae and Ophiderinae, including in the latter, the Rivulinae, another subfamily recognised mainly on the basis of tympanal characters. Heslop's reasoning probably coincided with that of Forbes (1954) on the same subject. However, Heslop did separate *Scoliopteryx* into the Gonopterinae. Franclemont & Todd included this genus in the Catocalinae. The Plusiinae, Acontiinae, Sarrothripinae and Acronictinae were recognised by both systems in equivalent terms (allowing for Heslop's inclusion of *Telesilla* [*Eucarta*] in the Plusiinae and his separation of the sarrothripines, together with the Westermanniinae [Chloephorinae], into the family Hylophilidae).

Within the trifines, the amphipyrine genera were divided into four subfamilies by Heslop. Of

these, the Apameinae and the Nonagriinae, are approximately equal to Franclemont & Todd's Apameini, although this tribe also includes *Hydraecia*, a genus Heslop placed in the Amphipyrinae. The second two of Heslop's subfamilies, the Amphipyrinae and the Caradrininae, roughly equate to Franclemont & Todd's Amphipyrini, with a few exceptions (e.g. *Prodenia* [*Spodoptera*] *litura*, which is in Heslop's Apameinae).

The cuculliine genera were placed by Heslop into three subfamilies. The Cuculliinae is equivalent to Franclemont & Todd's Cuculliini, while the Dasypoliinae and Xyleninae combined approximate their Xylenini. Interestingly, if *Jodia* and *Eupsilia* are incorporated from the Xyleninae, the Dasypoliinae equates to Forbes' (1954) Antitypini. The residual xylenines are then equivalent to Forbes' Lithophanini.

Heslop divided the hadenines into four subfamilies, all of which are included in Franclemont & Todd's Hadeninae: Hadenini. The two concepts of the subfamily Heliothinae agree although a more accurate equivalence would be between Heslop's Heliothinae and Franclemont & Todd's Heliothinae: Heliothini.

There are no North American representatives of those genera (*Mesogona, Euschesis* [*Noctua*, part], *Noctua* and *Lampra* [*Noctua*, part]) that Heslop placed in the Noctuinae, and thus his Agrotinae equates with the Noctuinae of Franclemont & Todd. However, on nomenclatural grounds, the Noctuinae (or at least *Noctua*) would belong in the Noctuini of Franclemont & Todd, which also includes several agrotines sensu Heslop. The two systems are therefore in disagreement. Forbes (1954) had already noticed this discrepancy between the European and American systems and considered the reason to be that 'European tradition has treated the whole group [Noctuinae] as a single genus, except a few species (not in fact closely related to each other) with yellow hindwings. There is no agreement [with his classification] as to this subdivision'.

However, overall and considering that the two systems are based upon more or less exclusive faunas, the classifications of Heslop (1960) and Franclemont & Todd (1983) are remarkably similar. It seems likely that a reassessment of the European fauna along the lines of that of North America would result in relatively few changes in subfamily/tribal placings with respect to Heslop's groupings. The inescapable conclusion is that the English amateur lepidopterists, in refusing to accept Hampson's system, and choosing to follow Kirby and Heslop instead, were more correct than perhaps they imagined.

Quo vadis, *Noctua*?

Introduction

That the higher classification of the Noctuidae is in disarray and in need of extensive re-evaluation is probably the only point on which all workers in the field agree. The Hampsonian system still maintains a considerable influence, despite many efforts to loosen its stranglehold, and in this respect very little advance has been made since 1920. However, current changes in attitudes probably mean that the days of the Hampsonian system *per se* are numbered, although there remains a vast amount of work to be done before an adequate replacement can be proposed.

To this end, I will first consider the individual subfamilies, illuminating those areas where I consider future research could be most usefully directed. Secondly, I present an outline cladistic analysis of the higher classification of the Noctuidae. This should not be considered as a 'new system', but merely as the first step towards the production of one. I do not expect everyone (or even anyone) to agree with all of my interpretations and conclusions, but I hope the result will be to generate renewed interest in noctuid higher systematics.

The individual subfamilies

Arctiidae: Aganainae. This group of moths has been consistently placed in the Arctiidae or else treated as a separate family closely related to the arctiids. Its importance regarding the higher systematics of the Noctuidae lies in its possible future transfer to that family.

A relationship between the Noctuidae and the Aganainae was first tacitly suggested by Gardner (1941) on the basis of larval characters. The two current aganaine species that he examined, *Hypsa* [*Asota*] *alciphron* and *H.* [*Psephea*] *ficus*, agree with the Noctuidae in having a single subventral seta on the meso- and metathorax (but see below). This contrasts with the bisetose condition found in the Arctiidae (the third 'aganaine' examined by Gardner, *Digama hearseyana*, which has a bisetose SV group, is currently placed in the Arctiinae). However, Gardner refrained from uniting the Noctuidae and Hypsidae [Aganainae], mainly because the latter lacked the ventral prothoracic gland found in the larvae of the former.

The discovery of the tymbal organ in the Arctiidae (Forbes & Franclemont, 1957; Blest *et al.*, 1963) provided a potential apomorphy by which the family could be characterised. However, its occurrence is not universal. The structure is conspicuously absent in the aganaines and a few wasp-mimicking ctenuchines (A. Watson, pers. comm.). It can be argued that the loss of the tymbal organ (and also the tympanal organ in a few species) in the latter group is concurrent with the general reduction and high degree of modification of the thoracic sclerites that has occurred in order to produce the hymenopteran facies. Tymbal loss cannot be so convincingly argued for in the aganaines, especially as it is lacking in all genera and not just a few as in the Ctenuchinae. Thus, if the Arctiidae were to be redefined, employing the presence of the tymbal organ as a synapomorphy, then the Aganainae would have to be excluded. Franclemont & Todd (1983) considered the aganaines to be 'probably an aberrant group of Noctuidae'. However, the aganaines have a pre-spiracular tympanal hood (Richards, 1932), and for this reason, I would choose to exclude them also from the Noctuidae (see Herminiinae below). The net result of these character interpretations would be the reinstatement of the Aganaidae as a separate family.

Herminiinae. Recognised as a distinct subfamily of noctuids by several pre-Hampsonian authors (e.g. Herrich-Schäffer, 1845; Grote, 1890; Smith, 1895), the Herminiinae were considered by Hampson as part of the Hypeninae. Forbes (1918) resurrected the subfamily on the grounds of the possession of a pre-spiracular tympanal hood but the exact position of the Herminiinae within the Noctuidae remained unsettled.

The primitive position of the hood was used by Kiriakoff (1963) to argue for the exclusion of the Herminiinae from the Noctuidae and their placement within a more-inclusive 'Arctiinae'. This conclusion, however, is disputed. Richards (1932) did not consider that the Herminiinae were the most primitive noctuids, on the grounds that the 'basal group' of genera (*Paraherminia* [*Paracolax*] and *Dercetis* [*Redectis*]), which were determined as the most primitive herminiines on other characters, had the spiracle 'slightly under (ventro-anterior to) the greatly reduced hood'. Thus, Richards implicitly treated the pre-spiracular hood in the herminiines as a character reversal, a position supported recently, without further elaboration, by Franclemont & Todd (1983). I remain unconvinced and maintain that the herminiine pre-spiracular hood does represent the plesiomorphic state. If this is accepted, then, in the absence of other evidence to the contrary, the subfamily must be considered to form the sister-group of the remaining noctuids, and represents an analogous situation to that between the Arctiidae and Aganainae. If the Noctuidae were to be defined by the possession of a post-spiracular hood, the herminiines would have to be excluded. Characterisation of the resultant 'Herminiidae' would be possible on the basis of the swollen metepimeron ventral to pocket IV and perhaps the modifications of the forelegs and antennae in the males.

The results of a cladistic analysis under the alternative interpretation of polarity are less satisfactory. Following the strict cladistic approach to loss characters (Patterson, 1982), reversion of the tympanal hood to a pre-spiracular position could not be used to justify the monophyly of the Herminiinae and would also cast doubt on the use of the post-spiracular hood to characterise the family Noctuidae. If this latter character state was then rejected, we should be left in the extremely unsatisfactory position of having a family of 25,000 species *completely uncharacterised*.

Cladistics aside, however, there is little doubt that a pre-spiracular hood is a good diagnostic character for recognising the herminiines (assuming that they can be differentiated from the

aganaines). Their separation from the other 'deltoid' groups has so far only been performed for the North American fauna.

Rivulinae. First proposed by Richards (1932), and then also including the genera currently assigned to the Hypenodinae (q.v.), the Rivulinae was interpreted as being the most primitive noctuid subfamily. However, it was also the most difficult for Richards to characterise and thus its status is highly questionable. Forbes (1954) rejected the Rivulinae, referring most of its genera to the Erebinae, as his third miscellaneous series. Likewise, Kiriakoff (1960) considered the Rivulinae to be insufficiently differentiated and placed both it and the Hypeninae in the Catocalinae-Erebinae complex. Recently, only Franclemont & Todd (1983) have employed the group.

At present, there appear to be no good characters on which to base the Rivulinae. Within the subfamily, Richards included those 'primitive' noctuids that could not be placed in either the Herminiinae or Hypeninae. The rivuline genera were thus characterised by a post-spiracular hood, unlashed eyes and short labial palps, characters that can all be interpreted as inapplicable at the level of universality relevant to the Rivulinae. Thus, the monophyly of the subfamily is unsubstantiated and it remains to be seen whether future studies will reveal any additional characters to suggest the Rivulinae is not a non-group.

Hypenodinae. Like the preceding two subfamilies, the Hypenodinae had been recognised only in the North American fauna. Characterisation of the group is weak. Richards (1932) included the hypenodine genera in the Rivulinae, which, given the vague nature of that group, is unsatisfactory. Forbes (1954) defined the hypenodines primarily on the lack of ocelli but, as mentioned above, such a feature is inadmissable in a strict cladistic framework. Other unifying characters may exist and were hinted at by Forbes (the subfamily is 'rather homogeneous in other structures'; 1954: 381) but their exact nature is unknown. Overall, while it remains possible that the Hypenodinae is a real entity, at present it cannot be stated with certainty. Further work on other faunas is necessary before a definitive conclusion can be reached.

Hypeninae. The Hypeninae was characterised by Hampson primarily by the hindwing vein M_2 arising from well above the lower angle of the cell and running parallel to M_3. Under such a definition, the subfamily also included the hypenodines and the herminiines.

Richards (1932) found the Hypeninae (s.str.) to be reasonably well characterised tympanally, and that, in addition, they possessed lashed eyes. The latter state is also found in the Plusiinae, Cuculliinae and the ophiderine *Scoliopteryx*. The tympanum and larvae of the last genus also resembled those of the Hypeninae (Richards, 1932: 14). Forbes (1954) added the character state of 'long and obliquely porrect [palps], normally twice as long as [the] head, with a rather long, porrect third segment'. Although it is probable that the Hypeninae, as restricted by Richards and Forbes, and employed recently by Franclemont & Todd (1983), does represent a monophyletic unit (sensu Farris, 1974), more work remains to be done. Further studies of the other deltoid subfamilies are also required in order to clarify the interrelationships of these much underworked and neglected yet phylogenetically important noctuids.

Catocalinae. The general consensus of opinion, faunal advantages notwithstanding, is that the division of this very large group of moths into the Catocalinae and the Ophiderinae, on the basis of mid-tibial spining, is entirely artificial and should be abandoned. However, the result of such action is a subfamily containing in excess of 10,000 named species, and probably many more awaiting discovery and description. Subdivision of this large group is therefore necessary. There are homogeneous groups of genera contained within the Catocalinae (s.l.); based around, for example, the genera *Catocala, Erebus, Parallelia, Anomis* and *Drasteria*, which can be defined by various structural features. However, the genera concerned represent only a very small proportion of the subfamily and the work required to completely order the Catocalinae (s.l.) is immense. Doubtless, further knowledge of the immature stages will prove invaluable – for

example, the Anomiini have malvaceous-feeding larvae; Forbes (1954: 367) – but so few are currently known that even their potential is largely unknown.

What is required is a piecemeal dissection of the group; the removal of the homogeneous generic groupings, perhaps as provisional tribes; followed by studies of the numerous isolated genera; leading finally to a coherent system. The task is so vast as to almost deny the possibility of success, especially when it is remembered that the Catocalinae may be polyphyletic with respect to the Hypeninae, Rivulinae, Hypenodinae and Acontiinae. Nevertheless, the attempt must be made, for the current state of knowledge, Richards' and Forbes' work on the North American fauna aside, is negligible.

Plusiinae. Of this subfamily, Richards (1932) stated that 'this is the most homogeneous and distinct of all the quadrifid groups'. Certainly, the plusiines have been recognised from the very earliest days of noctuid systematics as a natural group, but even so, their separation from the other subfamilies has been difficult. To Hampson, the plusiines were the lashed-eyed, non-deltoid, quadrifine noctuids. However, as previously noted, exceptions to this rule exist. Both *Scoliopteryx libatrix* and *Phyprosopus callitrichoides* have lashed eyes, while the eyes of the plusiine genus *Pseudeva* 'do not appear to be lashed' (McDunnough, 1944: 213).

Mosher (1916) found that the pupae of the Plusiinae showed a number of differences from those of other noctuids, most notably in the position of the labrum and the ventral extension of the wings and proboscis beyond the posterior margin of abdominal segment 4. The Plusiinae were further characterised by Richards (1932), who discovered that its members possessed a double tympanic hood and a swollen metepimeron formed by a greatly enlarged pocket IV.

Recently, Eichlin & Cunningham (1978) proposed three tribes within the Plusiinae. Of these, the Abrostolini is the best candidate for monophyly, based on the form of the clavus in the male genitalia. The Argyrogrammini is demonstrably paraphyletic, while there are doubts as to the monophyly of the Plusiini (Eichlin & Cunningham's 'Autographini') because it is primarily based on a character loss (absence of prolegs on abdominal segments 3 and 4). However, this is perhaps excusable given that the authors did not propose a cladistic classification. All three tribes may yet prove to be monophyletic but the study needs to be extended to the tropical faunas before this can be confirmed.

As to the position of the subfamily within the Noctuidae, the Plusiinae lack the proposed apomorphies of the Catocalinae (the fused pleural sclerite, J. D. Lafontaine, pers. comm.; and the bloom on the pupa, Mosher, 1916) and so it is likely that their affinities will prove not to be with that subfamily. It is possible that the plusiines will be demonstrated to be related to certain trifine groups, possibly parts of the Cuculliinae, Amphipyrinae or Heliothinae (see also below), but this is presently speculative.

Stictopterinae. Hampson characterised this subfamily primarily by the simplified female frenulum (the frequently used description 'single' is misleading, as the frenulum in female strictopterines often consists of more than one bristle, which are closely appressed and very difficult to discern; A. H. Hayes, pers. comm.) and the presence of tufts of raised scales in the forewing cell. Richards (1932) considered the stictopterines to be very close to the plusiines but he only examined two species of the genus *Stictoptera* (*S. melanistis*, from the Old World, and *S. clara*, a Neotropical species that should be referred to a separate genus; J. D. Holloway, pers. comm.). Both were found to possess a tympanal hood with a ventral second lobe. In *S. melanistis*, this lobe was large enough to give the impression of a double tympanal hood, similar to that found in the Plusiinae.

The lack of stictopterines in North America has resulted in very little structural information being collected for the group (*S. clara* probably never reaches north of Mexico and Cuba, despite a paratype of *S. phryganealis* [a synonym of *S. clara*] in the BMNH bearing the locality 'West Coast of America'. This designation of Walker's often meant the west coast of *Central* America, or even the Galapagos Islands; Hayes, 1975: 165–7). This situation will be partially alleviated in a forthcoming revision of the Bornean stictopterines by J. D. Holloway. Nevertheless, further study is required to ascertain the interrelationships of the genera and the position of

the subfamily within the Noctuidae. It is likely that the Stictopterinae will prove to be closely related to the Plusiinae, but whether it represents the sister-group of the latter remains to be demonstrated conclusively.

Euteliinae. Unlike many other noctuid subfamilies, several good apomorphies are known for the Euteliinae. However, none of these occurs in the morphology of either the tympanal organs or the larvae. Richards (1932) found that the tympana of the euteliines could be derived from either the catocaline (s.l.) or the acontiine types and he was unable to place them on his phylogenetic tree (Fig. 3). Similarly, Gardner (1948*a*) discovered no unifying characters in the larvae. In contrast, he (Gardner, 1948*b*) found a combination of characters in the pupae that sharply defined the Euteliinae, of which the complete lack of a cremaster was the most characteristic (although the cremaster is also absent in the Sarrothripinae and Chloephorinae; Mosher, 1916; Gardner, 1948*b*). Forbes (1954) noted that the larvae were almost completely restricted in their foodplants to members of the Anacardiaceae (although some feed on Combretaceae and Hamamelidaceae; Mell, 1943) and that the adults typically 'rest with the fore wings crumpled and partly rolled about the hind wings, and standing out obliquely to the strongly upcurved abdomen'.

The subfamily is probably monophyletic on the basis of the above characters and other, as yet undescribed, structural features (J. D. Holloway, pers. comm.). The problem of where the Euteliinae fit within the Noctuidae remains, however. The reduced female frenulum could represent a synapomorphy linking the euteliines and stictopterines, but as a loss character, it does not form very strong evidence. Similarly, the lack of a cremaster, a feature also shared with the Sarrothripinae, Chloephorinae and possibly the Nolinae is also weak. Otherwise, the euteliines are very distinct and their interrelationships with other noctuid groups are far from clear.

Chloephorinae. With the transfer of *Bagisara* to the Acontiinae (Heinrich, 1926) or Amphipyrinae (Forbes, 1954), and *Ipimorpha* to the Amphipyrinae (Forbes, 1954), the Chloephorinae ceased to be represented in the North American fauna. Consequently, little is known of the morphology of the group. Richards (1932) found the chloephorines combined the characters of both the acontiine tribes (Erastriini [Eustrotiini] and Tarachini [Acontiini] and believed the group to be derived from the higher Acontiinae. Mell (1943) considered the Chloephorinae to be indistinct from the Sarrothripinae and treated the two groups as a single subfamily. A study of the larvae led Gardner (1946*a*; 1948*a*) to disperse the genera of chloephorines widely among his noctuid groups but subsequent examination of the pupae and cocoons (Gardner, 1948*b*) caused him to revise his decision. He finally placed all the chloephorines in a single group near the sarrothripines, although he considered *Acontia* [*Xanthodes*] to perhaps belong elsewhere.

There appears to be little doubt now that the Chloephorinae is very closely related to the Sarrothripinae. They share such probable apomorphies as a bar-shaped retinaculum in the males and the characteristic boat-shaped cocoon. Whether the Chloephorinae deserves subfamilial rank (based at present on the lack of the tufts of raised scales in the fore-wing cell found in the Sarrothripinae – not only an absence but also a highly homoplasious character in that similar tufts occur in the nolines and stictopterines) or merely tribal rank within the Sarrothripinae, or whether, as Mell (1943) proposed, the two-way division itself is artificial and should be replaced, is as yet debatable.

Sarrothripinae. This subfamily was separated from the last by Hampson on the basis of the presence of raised scales in the forewing cell. Richards (1932) found that the Sarrothripinae and Chloephorinae were tympanally very close and, like Hampson, considered the former to be derived from the latter. Gardner (1948*b*) could find only minor differences between the two subfamilies while Forbes (1954) suggested that the Sarrothripinae intergraded in the Old World with the Nolinae.

Apart from Mell's (1943) subdivision, the Sarrothripinae had always been treated as a single homogeneous entity. However, Franclemont & Todd (1983) divided the subfamily into three

tribes: the Risobini, the Sarrothripini and the Collomenini. Forbes (1954) considered *Baileya* (the sole member of the Risobini) to be totally isolated within the North American fauna and most closely allied to the Old World *Risoba*. The larvae of both genera were said to resemble those of the Euteliinae and might prove to form some sort of link between the two groups. The justification of the Collomenini is not clear. The two constituent genera (*Collomena* and *Motya*) were not dealt with by either Mell or Forbes, and Franclemont & Todd (1983) do not give any reasons for employing the tribe.

Nolinae. The Nolinae also has affinities with the Sarrothripinae. Forbes (1960) derived the former from the latter, while Richards (1932) (Fig. 3) preferred an independent development from the Acontiinae. However, the boat-shaped cocoon of the nolines, together with tufted setae (similar to those found in certain sarrothripines; Forbes, 1960: 52) point towards a relationship with the Sarrothripinae, and hence the Chloephorinae. There appears to be a potentially monophyletic group of three subfamilies, which may also possibly be related to the euteliines, through the Risobini. However, such a relationship is as yet largely unverified.

Acontiinae. This subfamily was Hampson's least well-defined group as adults, falling as it did across the trifine-quadrifine boundary. However, he did note that 'the larvae of such as are known [have] the anterior [pair of] prolegs aborted, which is the essential distinction between the two subfamilies' [Acontiinae and Amphipyrinae + Acronictinae]. This character was of limited use, however, because so few acontiine larvae were known at the time, and reduction of the anterior prolegs is widespread in other noctuid subfamilies. Also, there are several acontiines (e.g. *Neoerastria* [*Homophoberia*]) in which all the prolegs are present (Forbes, 1954: 270).

Richards (1932: 23) considered the acontiines 'to have been derived from some point between the Rivulinae and Hypeninae with *Eublemma* [*Eumicremma*] as the connecting link' (but see Fig. 3), and which then gave rise to the sarrothripine-chloephorine series, the Nolinae, the trifine subfamilies and the Agaristinae. The Acontiinae itself was divided into three sections: *Eublemma* [*Eumicremma*], the Erastriini [Eustrotiini] and the Tarachini [Acontiini]. Of the two tribes, probably only the second is monophyletic on the basis of the enlarged, chitinised alula. The Eustrotiini was characterised by the lack of such an alula and is therefore undoubtedly at least paraphyletic.

Forbes (1954) characterised the Eublemmini (*Eublemma* [*Eumicremma*]) using probable plesiomorphies ('pocket IV double as in the deltoids, hood and alula normal, no corona or penicillus' [on the valve of the male genitalia]) and did not improve upon the definition of the Erastriini [Eustrotiini]. Franclemont & Todd (1983) largely accepted Richards' and Forbes' classification but employed two additional monobasic tribes, the Cydosiini and the Bagisarini, erected to contain two presumably, somewhat aberrant genera.

The higher classification of the Acontiinae leaves much to be desired. Only the Acontiini and the monobasic tribes are likely to be monophyletic. The Eustrotiini appears to represent a heterogeneous assemblage of genera that do not fit any of the other tribes. However, the crucial position of the subfamily in understanding the higher systematics of the Noctuidae as a whole means that a thorough (cladistic) analysis should be accorded high priority.

Pantheinae. As adults, apart from dubious differences in hindwing venation, the members of the Pantheinae share the same Hampsonian defining characters as the Hadeninae: unspined tibiae and hairy eyes. The larvae, however, are quite different, being clothed, except for *Raphia*, in dense tufts of secondary setae on the body and head. In the latter respect, the Pantheinae differ from the Acronictinae. Richards (1932) found them tympanally very homogeneous but highly isolated from the rest of the noctuids; so much so that he was unable to even tentatively assign them a place on his phylogenetic tree. Forbes (1954) also noted the well-defined nature of the Pantheinae, although he had reservations regarding *Raphia*. This genus corresponded to the other pantheines in its tympanum, wing venation and general facies, but differed in the microscopic hair on the eyes and the larva lacking secondary setae. Nye (1975), following

Hampson, placed *Raphia* in the Ophiderinae. *Raphia* may belong in the Pantheinae, but it could equally belong elsewhere and only a thorough understanding of the rest of the family will finally resolve the question.

Franclemont & Todd (1983) follow Forbes (1954) but also suggest the possibility of merging the Pantheinae and Acronictinae. If Richards (1932) were correct regarding the tympanal structure of the two groups, then such a move would be premature, which is not to rule it out. The two subfamilies were long considered closely related (e.g. Smith & Dyar, 1898) and the presence of secondary setae in the larvae may be a synapomorphy. However, Mosher (1916) noted that the pupa of *Charadra deridens* (the only species examined) was more arctiid than noctuid, in the shape of the body, the presence of setae arranged around the scars of the larval verrucae, the absence of an epicranial suture and in the labial palps and prothoracic femora being visible. However, the cremaster is more noctuid than arctiid, in being long and provided with hooked setae. Additionally, the pantheines have never been recorded as possessing tymbal organs. The sum total of these characters, together with Mosher's highly restricted sample, suggest that, until further information has been gathered, the pantheines are best left in the Noctuidae. Their position with regard to the other subfamilies, however, remains unknown.

Acronictinae. The Acronictinae is the first of the trifine subfamilies, all of which are highly uniform structurally. This has resulted in much confusion in their classification and has led to an over-reliance upon superficial characters (hairy/lashed eyes, spined tibiae). However, some order can be discerned within the trifines and one group of genera that has long been recognised as a distinctive subgroup is the Acronictinae.

Originally, the acronictines were distinguished by the presence of secondary setae on the body of the larvae. The subsequent inclusion of the bryophilines confused matters, because the larvae of these genera possess only long, primary setae. Hampson placed no emphasis on larval vestiture and included the acronictines, together with the amphipyrines and certain heliothines in a more inclusive 'Acronyctinae', where they have generally remained.

Gardner (1946*a*) distinguished the acronictines as his group AI. He also included the pantheine *Diphthera* [*Trichosea*] *champa*; the amphipyrine *Cetola dentata* and the ophiderine *Thiacidas postica* (this genus appears superficially to resemble *Raphia* and may thus be better placed in the Pantheinae – assuming *Raphia* belongs in that subfamily). Examination of the pupae led Gardner (1948*b*) to exclude *Cetola* from the Acronictinae and he placed it instead in the Amphipyrinae. Mosher (1916) found the pupae to be of little use in distinguishing the Acronictinae; so much so, that she also included an amphipyrine (*Achatodes*) and three catocalines (s.l.) (*Homopyralis* [*Metalectra*], *Anomis* and *Plusiodonta*). However, she was well aware of the unnatural nature of this grouping.

Forbes (1954) followed Hampson and treated the acronictines as a tribe (the Apatelini) within his second series of 'Acronyctinae', but the trend was reversed by Franclemont & Todd (1983). They reinstated the Acronictinae as a separate subfamily, containing two tribes, the Acronictini and the Bryophilini. As mentioned above, Franclemont suggested that the trifine noctuids might be better treated as comprising only two subfamilies: the Acronictinae (including the Pantheinae) and the Noctuinae (comprising the remainder). Unfortunately, he did not elaborate on his reasoning.

The Acronictinae, as restricted by Franclemont & Todd, probably represents a monophyletic unit but its limits are presently poorly defined. Whether it indeed is related to the Pantheinae, or is a convergent offshoot from somewhere within the Amphipyrinae, remains to be discovered.

Agaristinae. For a long time, these brightly-coloured, largely diurnal and aposematic moths were accorded family rank near the Arctiidae. However, Mosher (1916) could not discover any differences in the pupae to distinguish the agaristines from the Noctuidae and thus placed them in the latter as a subfamily. Richards (1932) found the agaristine tympanal organ to be similar to those of the Acronyctinae [Acronictinae + Amphipyrinae], although the counter-tympanal cavities of the agaristines were much enlarged. Nevertheless, he retained the family status of the group and considered the agaristines to be derived from the Acronyctinae (Fig. 3).

Gardner (1946*b*) examined two agaristine genera (*Aegocera* and *Eusemia* [*Episteme*]) and placed them in his group AVI, together with *Callyna* (Amphipyrinae), *Tiracola* (Hadeninae) and *Churia* (Chloephorinae). In his subfamily summaries, Gardner (1948*a*) listed the Agaristinae between the Noctuinae and the Cuculliinae, suggesting that he considered the group to be merely aberrant trifine noctuids. Forbes (1960) retained the family status whereas Franclemont & Todd (1983) treated them as a noctuid subfamily. It is probable that the Agaristinae is monophyletic, although the involvement of mimicry might complicate superficial resemblances. The relationships of the subfamily to other trifine groups is currently poorly understood.

Amphipyrinae. To Hampson, this subfamily (including the Acronictinae and the *Pyrrhia*-group heliothines) was characterised entirely by absences: hindwing vein M_2 reduced, the tibiae unspined and the eyes bare and unlashed. As such, the group can be seen to be a prime candidate within the Noctuidae for paraphyly or polyphyly. Unfortunately, like the Catocalinae (s.l.), the large size of the group (it contained nearly 2,400 species in Hampson's *Catalogue*, a number that has considerably increased since; Forbes, 1954) has resulted in a long period of classificatory stasis. Richards (1932) found a high degree of uniformity in the tympanum and could not suggest any interrelationships beyond that they appeared to be derived from the higher Acontiinae, a group that itself is probably not monophyletic.

Gardner (1946*a, b*; 1947; 1948*a*) found a great deal of diversity within the larvae and allocated amphipyrines to his groups AI, AII, AVI, BI and C. In contrast, the pupae of this subfamily were, for the most part, indistinguishable from those of the Hadeninae, Noctuinae and Heliothinae that he examined.

The first attempt to subdivide the Amphipyrinae, in which the characters used were stated, was provided by Forbes (1954). On the basis of the genitalia and larvae, he erected two series, each divided into several tribes. Franclemont & Todd (1983) reduced the number of tribes to four. The Apameini corresponded to Forbes' first series less the Prodeniini. This latter tribe, together with many of Forbes' isolated genera, formed the Amphipyrini, while the Stiriini was largely unchanged. Franclemont & Todd's fourth tribe, the Nocloini, the basis for which is unclear, contained seven genera not dealt with by Forbes.

Of these four tribes, the Stiriini is almost certainly monphyletic (Hogue, 1963) and the Apameini (and Nocloini?) may also prove to be. The Amphipyrini appears to be a somewhat more restricted 'dustbin' than was the Amphipyrinae and is therefore likely to be at least paraphyletic. It may even be polyphyletic given that the other trifine subfamilies are thought to have arisen from within its limits, as presently defined.

Cuculliinae. The Cuculliinae is also a prime candidate for having a polyphyletic origin (Forbes, 1954). It was circumscribed by Hampson on the basis of bare, lashed eyes and unspined tibiae, not the most convincing of characters, especially as, venation apart, it applies equally well to the majority of the Plusiinae. Lack of material prevented both Mosher (1916) and Gardner (1948*a*) from reaching more than highly tentative conclusions regarding both the internal and external relationships of the Cuculliinae based on larvae.

Forbes (1954) divided the subfamily into two series, each comprising three tribes, which he thought to have been independently derived from the 'Acronyctinae'. The Cuculliini, Oncocnemidini and Psaphidini were considered to be related to certain Stiriini (q.v.) and the genera *Oxycnemis* and *Catabena* (the latter an 'isolated genus' of acronyctines, the former not mentioned elsewhere). This latter relationship was recently strengthened by the inclusion of *Catabena* and *Oxycnemis* in the Oncocnemidini (Franclemont & Todd, 1983). The remaining three tribes, the Lithophanini, Cleocerini and Antitypini, apparently showed affinities with such genera as *Andropolia*, *Rhizagrotis* and some elements of the *Apamea-Septis* complex (all of which are currently placed in the Apameini; Franclemont & Todd, 1983). The latter authors retained the Cuculliini, Oncocnemidini and Psaphidini but considered the other three as constituting a single tribe, the Xylenini. In addition, *Feralia* was placed in the monobasic Feraliini.

Given the highly uncertain nature of the trifine subfamilies in general, to find the Cuculliinae

polyphyletic would be no great surprise. Of the constituent tribes, the Psaphidini (fore-tibial modification) and the Feraliini (by virtue of it containing a single, assumed monophyletic genus) are probably monophyletic taxa. The Cuculliini and Oncocnemidini taken together may also prove monophyletic but the latter may be paraphyletic with respect to the former ('they tend to intergrade in Europe'; Forbes, 1954: 122). The Xylenini, as currently conceived, is probably paraphyletic, although the Lithophanini (sensu Forbes, 1954) may prove a monophyletic unit, based upon the form of the digitus in the male genitalia and the biological characteristic of an autumn adult emergence followed by hibernation. These tentative conclusions are unaffected by the nature of the Cuculliinae as a whole.

Hadeninae. The hadenine genera were originally separated into a number of subfamilies by early authors (e.g. the Orthosiinae, Leucaniinae, Hadeninae; see also Heslop, 1960). However, they were all brought together into a single trifine subfamily by Hampson, defined by hairy eyes and unspined tibiae. As with the other trifine groups, tympanal organs and immature stages provided little information. Mosher (1916) characterised the Hadeninae by pupae possessing 'stout straight setae or spines at the caudal end of the body'. However, she also included the heliothines *Chloridea* [*Heliothis*], *Pyrrhia* and *Rhodophora* [*Schinia*], the noctuine *Lycophotia* and the amphipyrines *Eriopus* [*Callopistria*] and *Laphygma* and *Prodenia* [both *Spodoptera*].

Forbes (1954) recognised three general facies within what he considered 'a homogeneous group', but also noted that a large proportion of the genera did not fit into any of them. Consequently, he did not formally subdivide the hadenines, unlike Franclemont & Todd (1983), who recognised three tribes. The Glottulini comprised only *Xanthopastis*, an aberrant genus Forbes considered might not be closely related to the other hadenines. The Eriopygini contained *Orthodes, Tricholita* and their relatives, while the Hadenini consisted of the residue. The Glottulini are probably monophyletic given, for example, their amaryllidaceous-feeding larvae (this tribe undoubtedly also includes the Old World genus *Brithys*). From the available information, the basis of the Eriopygini is unknown and consequently its status cannot be commented upon. Such is therefore also the case for the Hadenini but it is almost certainly at least paraphyletic, even assuming the Eriopygini to be adequately characterised. Within the Hadeninae, there are 'centres of monophyly', around such genera as *Xanthopastis, Mythimna, Hadena* and *Orthosia*, but their limits and interrelationships have yet to be established.

Noctuinae. This was the fourth and last trifine subfamily recognised by Hampson, on the basis of spined tibiae. Both Mosher (1916) and Gardner (1946*b*; 1948*a*) found no characters by which they could distinguish the larvae and pupae of the noctuines from those of most other trifine genera. The heliothine section of the Agrotinae (sensu Hampson) had long been recognised by early authors as a discrete group but only slowly re-emerged as a distinct entity, which varied from being classed as a tribe of the Noctuinae (Forbes, 1954) to a separate subfamily that was isolated from the Noctuinae (e.g. McDunnough, 1938). Discussion of the 'heliothine Noctuinae' is deferred to the next section.

The remaining genera of Noctuinae were split by Heslop (1960) into two groups, following European tradition, one (Noctuini) characterised by yellow hindwings, the other (Agrotini) by hindwings of a different colour (usually brown). Forbes (1954) disagreed with this system, preferring instead to recognise three informal groups based around *Agrotis, Peridroma* and *Noctua*, which were formalised by Franclemont & Todd (1983) as the Agrotini, Aniclini and Noctuini respectively. In addition, they recognised a fourth tribe, the Ufeini, to accommodate the aberrant genus *Ufeus* ('The genus is not really an Agrotid, but fits no better elsewhere'; Forbes, 1954: 74).

The three large tribes are relatively well defined by larval and genitalic characters but it is not clear how well these would stand up to a critical cladistic analysis. Indeed, the monophyly of the Noctuinae itself has yet to be adequately demonstrated.

Heliothinae. The Heliothinae was formed largely from the union of two subgroups of trifine noctuids, classified widely apart by Hampson, based around the genera *Heliothis* and *Pyrrhia*.

The former, because of their spined tibiae, were placed in the Noctuinae, while the latter, which lacked all Hampson's 'definitive characters', were relegated to 'acronyctine' obscurity.

However, the larvae of the Heliothinae are relatively distinctive. Their habit of feeding more or less exclusively on the flowers and fruits of low-growing plants had long been recognised, but this information was subsequently supplemented by structural features (Crumb, 1926; 1956; Gardner, 1946*a*,*b*). Of prime importance among these were the biordinal crotchets, a feature that the group shares with most Plusiinae and some Cuculliinae.

The North American Heliothinae were revised by Hardwick (1970). He excluded *Grotella, Neogrotella* and *Hemigrotella* from the subfamily, because of their slender build, distinctly quadrifine hindwing venation and the presence of multiple cornuti on the vesica, features that Hardwick considered linked the three genera with the Stiriini. However, Franclemont & Todd (1983) retained them in the Heliothinae as the Grotellini, possibly as an interim measure.

The relationship between the Stiriini, the Heliothinae and, possibly, the Plusiinae warrants further consideration, due to its potential profound effects upon the higher classification of the Noctuidae generally. Hogue (1963) considered the Stiriini were derived from generalised noctuine stock via forms similar to either certain Heliothinae or Oncocnemidini, with the latter more likely (both groups possess an angled vesica bearing numerous cornuti). Furthermore, Hogue treated any resemblance to the Plusiinae to be entirely convergent.

Hardwick (1970) discussed the relationship between the Stiriini and the Heliothinae in considerable detail and concluded that there were 'a sufficient number of features in common to suggest some immediate common ancestry'. No mention was made of the Plusiinae with reference to a relationship with the stiriines and heliothines. That such a possibility can be entertained rests on somewhat equivocal evidence. Both the Heliothinae and the Plusiinae have larvae with biordinal crotchets, which could be interpreted as synapomorphic. However, the larvae of the tentative sister-group of the plusiines, the Stictopterinae, have uniordinal crotchets (Gardner, 1948*a*), while the larvae of most stiriines are unknown and the crotchets of such that are have never been examined. Biordinal crotchets may, therefore, be homoplasious in the two groups. Perhaps the only overall conclusion that can be reached, like so many concerning the higher classification of the Noctuidae, is that it all depends on the results of investigations yet to be done.

The higher classification of the Noctuidae – fact or fiction?

No adequate higher classification of the Noctuidae can yet be proposed that will serve as a replacement for the Hampsonian system. However, it is possible to construct a tentative cladogram (Fig. 4) to serve as a suitable starting-point. Only those apomorphies that can be reasonably positively identified are included, although those on several branches are highly suspect. The relative paucity of synapomorphies results in a number of extensive polychotomies and several of the groups being uncharacterised (see below). The individual branches, 1–34, will be discussed and justified seriatim, and their relative merits assessed.

1. The Arctiidae generally can be characterised by three apomorphies, none of which are present in all genera. Two are perhaps quite reliable: the presence of the tymbal organ (although this is absent/lost in some of the ctenuchines and a few other groups) and the presence of two subventral (SV) setae in the larvae on the meso- and metathorax. Only one SV seta is present in this position in the aganaids, herminiids and noctuids (Gardner, 1941), and examination of five notodontids (*Stauropus fagi, Notodonta dromedarius, Eligmodonta ziczac, Peridea anceps* and *Pheosia tremula*; Kitching, unpublished) showed these also possess only a single seta. The latter evidence was used in an outgroup comparison to establish the bisetose condition as apomorphic. The third arctiid apomorphy, a swollen hindwing vein $Sc + R_1$, is more uncertain, especially as 'swollen' has never been precisely defined.

2. No apomorphies have been discovered in the literature for the aganaid genera. As such, they are of uncertain position and it is possible for some to be more closely related to the

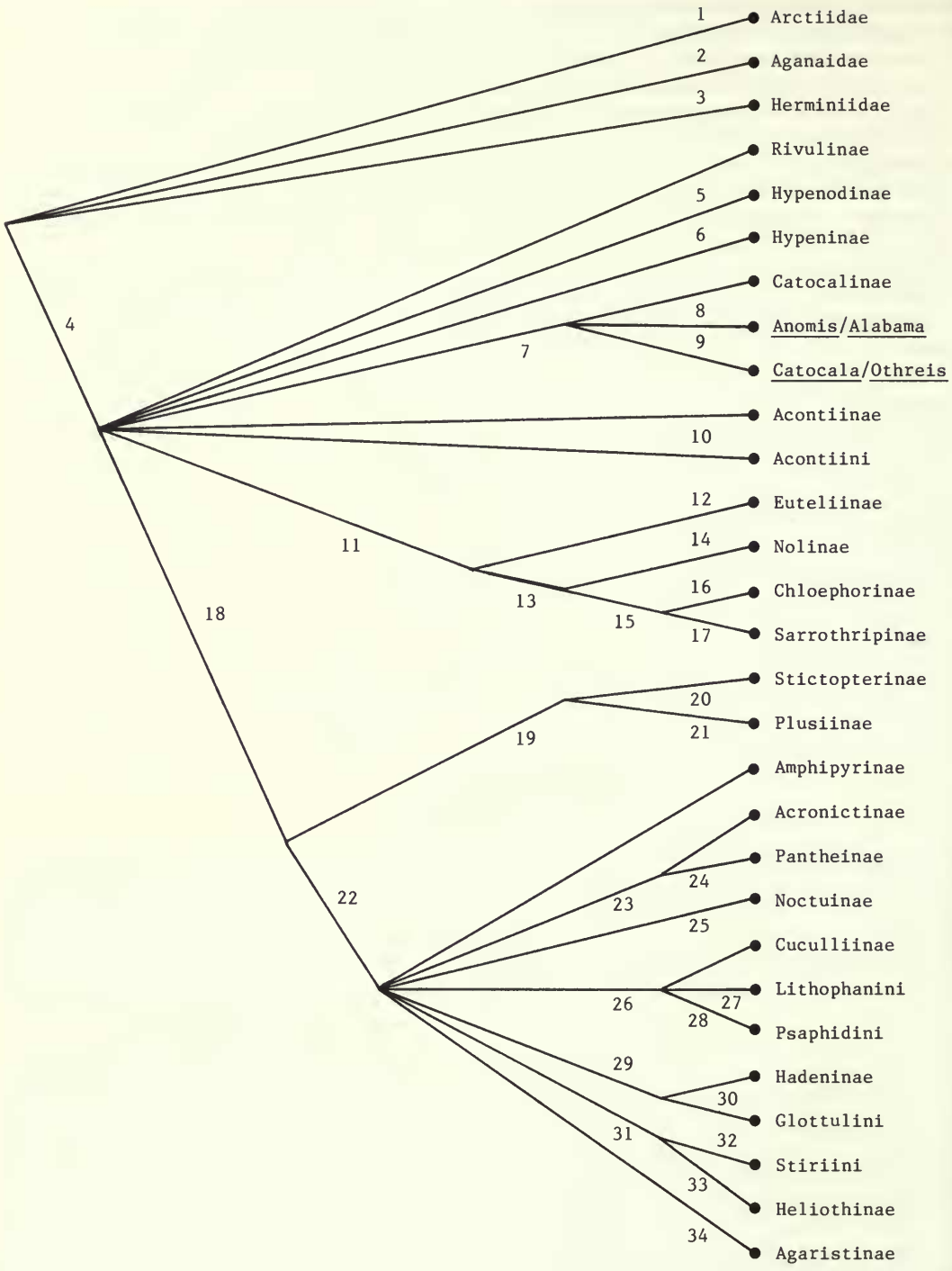

Fig. 4 Cladogram illustrating the relationships between the various noctuid subgroups. For details regarding the characters defining each of the numbered branches, 1–34, see pp. 223–226. Seven branches are undefined by apomorphies; those subtending the Rivulinae, Catocalinae, Acontiinae, Amphipyrinae, Acronictinae, Cuculliinae and Hadeninae. For discussion of the undefined branch 2, see pp. 214–215, 223–225.

arctiids and some to the noctuids. It may even be that some represent the sister-group of the herminiids.

3. The exclusion of the 'fan-foots' and their relatives from the Noctuidae (branch 4) is primarily on the basis of the plesiomorphic pre-spiracular hood. In addition, they may be characterised by two apomorphies: modified fore-tibiae in the males of most genera (although the exact nature of the modification is deliberately left unspecified) and a swollen metepimeron ventral to pocket IV.

4. The Noctuidae is restricted to those groups possessing a post-spiracular hood, although this is absent in the Pantheinae (q.v.) and is greatly reduced in many other genera scattered among the other subfamilies. These can be interpreted as secondary losses but require further analysis. Two uncharacterised paraphyletic/polyphletic assemblages are recognised within the heptachotomy that terminates branch 4, the Rivulinae and the Acontiinae.

5. The Hypenodinae are characterised by the lack of ocelli, an unsatisfactory situation but the best that can be done at present.

6. A similar situation pertains to the Hypeninae. Its putative apomorphies of long, 'deltoid' palps and lashed eyes are not particularly convincing.

7. The Catocalinae (s.l.) are better characterised (fused pleural sclerite in the male genitalia and pupa with a whitish bloom) but the majority of genera and species of this vast subfamily have yet to be examined, especially with regard to the pupal character.

8 & 9. These branches represent two of the many genus-groups that can be recognised in the Catocalinae (s.l.). *Anomis* and *Alabama* (the Anomiini of Forbes, 1954) are defined by an enlarged but unsclerotised alula and malvaceous-feeding larvae. *Catocala* and *Othreis* both possess a chitinous projection from the inner margin of the tympanal frame (the 'Bügel'; Eggers, 1919).

10. Of the acontiine groups, only the Acontiini is well-characterised: tympanal hood reduced/ lost, alula enlarged and sclerotised, male with paired anal hair-masses; cf. Euteliinae (Forbes, 1954: 271).

11. This branch includes four subfamilies, tentatively grouped on the absence of a cremaster. However, this has not been confirmed for the Nolinae. The Euteliinae also bear a general resemblance in venation and the larvae of certain sarrothripine genera (Forbes, 1954: 288).

12. The Euteliinae are perhaps the most well-defined subfamily of noctuids: frenulum reduced in the female; larvae feeding mainly on Anacardiaceae; pair of anal hair pencils present in the male; and the attitude of the adults at rest. There can be little doubt they represent a monophyletic taxon.

13. The Nolinae, Sarrothripinae and Chloephorinae are united by the common possession of a boat-shaped cocoon with a vertical exit slit.

14–17. Unfortunately, the relationships within the above group of subfamilies are unclear. The Chloephorinae and Sarrothripinae agree in the possession of a bar-shaped retinaculum in the male but the latter also agrees with the Nolinae in the presence of tufts of raised scales in the forewing cell. As the second character also occurs elsewhere in the Noctuidae (e.g. the Stictopterinae and the Plusiinae: Abrostolini), the first character is preferentially taken to represent a synapomorphy. However, it is probable that the group needs to be split up in a different manner, possibly along the lines suggested by Mell (1943). In addition, the nolines lack ocelli in the adult and have larvae with tufted setae.

18. The 'higher noctuids' can generally be characterised by the presence of a clavus in the male genitalia. However, this structure is absent in many genera and uncertainties regarding genitalic homologies decrease confidence in this character. Secondly, the larval silk-pore of

the included subfamilies is not concealed (Crumb, 1956) and may represent a good apomorphy, although the condition in the Stictopterinae is unknown.

19–21. The Stictopterinae and Plusiinae share a double tympanal hood and tufts of raised scales in the forewing cell (present in the Plusiinae only in the Abrostolini). The stictopterines can be distinguished by the reduced female frenulum and possibly by the caudal extremity of the pupa being produced as 'two divergent attenuated spines borne together on a thicker median stem' (Gardner, 1948*b*: 88). The plusiines are relatively well defined, with four apomorphies: lashed eyes, a metepimeral bulge formed by an enlarged pocket IV, biordinal crotchets in the larvae and pupae in which the wings and proboscis project beyond the posterior margin of abdominal segment 4 ventrally.

22. The subfamilies subtended by this branch, the 'Trifinae', are held together on rather dubious grounds. Of the obsolescent hindwing vein M_2, nothing more needs to be said. The tympanal organs of all forms (except the Pantheinae, see branch 24) are extremely uniform and similar to those of the 'higher Erastriinae' [Acontiinae] (Richards, 1932: 29). The exact nature of this homogeneity and whether it includes any structures that can be regarded as synapomorphies was not elucidated by Richards.

22–24. The Acronictinae and Pantheinae are grouped on the basis of the presence of secondary setae on the larval trunk. However, the absence of such setae in the Acronictinae: Bryophilini weakens this argument, and the two subfamilies may not be closely related at all. The pantheines are further distinguished by their hairy eyes, the presence of secondary setae on the larval head, the reduction/absence of the tympanal hood and the highly modified tympanal morphology (Richards, 1932: 28).

25–30. Three branches (25, 26 and 29) subtend three of the currently recognised trifine subfamilies, the Noctuinae, Cuculliinae and Hadeninae respectively. This was done, not because there are good synapomorphies for the included genera (the characters employed are the classic ones of spined tibiae, lashed eyes and hairy eyes), but because to omit them would create a vast, *uncharacterised* group of genera (cf. the Catocalinae). In addition, it is probable that some of the groups will eventually be able to be defined by good apomorphies. Two tribes are split out of the Cuculliinae: the Lithophanini (well-developed digitus in the male genitalia, adult emergence generally autumnal, followed by hiberation) and the Psaphidini (fore-tibia with a terminal claw on the inner side, usually with an oblique, flat plate continuous with it; Forbes, 1954: 127); and one tribe from the Hadeninae: the Glottulini (larvae brightly-coloured, black, transversely spotted with yellow/white; feeding on the bulbs of the Amaryllidaceae).

31–33. The amphipyrine tribe, the Stiriini, and the Heliothinae are associated by the clawed fore-tibiae (single in the former, multiple in the latter) and the larval preference for feeding on flowers and young fruits. The Stiriini are characterised by an angled vesica with multiple cornuti and a heavily chitinised frons in the adult, with a raised ring and various projections. The larvae of the Heliothinae have biordinal crotchets.

34. The final noctuid subfamily to be considered is the Agaristinae. This is a highly apomorphic group: counter-tympanum several times the size of the tympanal membrane; hood very reduced/absent; adults active by day, generally brightly coloured, usually with clubbed antennae; larvae also brightly coloured, feeding largely on Vitaceae and Onagraceae.

I do not claim that the apomorphies employed in Fig. 4 are all that could be used to reconstruct the higher classification of the Noctuidae. However, they do represent all those extracted from the literature in which I have more than minimal confidence regarding the polarity, although it must be remembered that few are known to be present in all members of the group that they are being used to characterise. Many more characters are known at the subfamily level (see, for example, those cited by Forbes, 1954) but their usefulness has yet to be assessed. In addition,

there are certainly a considerable number of features known that are as yet undocumented, which must therefore necessarily fall outside the scope of this analysis.

To return to the title of this section, it would perhaps be more appropriate to refer to the Hampsonian classification as 'classifiction'. The system proposed by Franclemont & Todd (1983), which ranks as the main contender as an alternative, has much to commend it. However, it is of limited application until extended to encompass the world fauna and, unfortunately, until such time as the defining characters/apomorphies of the included groups are reported, such development is impossible. That there is a higher classification for this group of moths is not in question, but until careful character analyses, performed within a cladistic methodological framework, are published, the present state of confusion will reign. I hope that noctuid systematists will rise to meet the challenge.

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Only the more important references to higher taxon names are included and those taxa mentioned in passing are omitted. The indexed authors are those whose works are discussed at length.